NORTH ATLANTIC RIGHT WHALE (*EUBALAENA GLACIALIS*) ACOUSTIC BEHAVIOR AND FEEDING IN CAPE COD BAY, MASSACHUSETTS

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ABSTRACT

Many species use acoustics for communication including whales, birds, elephants, frogs, primates, and insects (Payne 1971; Narins and Capranica 1978; Poole, Payne et al. 1988; Brown 1991; Hauser 1993a; Hauser 1993b; Hoy 2002). This study examines whether North Atlantic right whales (*Eubalaena glacialis*) use acoustic communication to advertise the availability of their primary prey, *Calanus finmarchicus*, a species of zooplankton. The North Atlantic right whale, a species numbering approximately 350 individuals, is one of the most endangered whales in the world (Clapham 1999). Currently the functional significance of right whales producing contact calls in the context of searching for food and feeding is not understood. The research described in the following pages is directed at exploring the relationship between North Atlantic right whale acoustic and feeding behavior. The acoustic data for the Cape Cod Bay (CCB) right whale acoustics and feeding research project has been collected using marine autonomous recording units (MARUs) developed by Cornell University (Clark 2002). The research focuses on the hypothesis: *North Atlantic right whales acoustically advertise food resources, thereby practicing reciprocal cooperation*. The prediction following this hypothesis is: *Within a given area, zooplankton density will be correlated to right whale call number*. The alternative hypothesis is: *North Atlantic right whales do not acoustically advertise food resources nor participate in reciprocal cooperation.* The prediction following the alternative is hypothesis: *within a specific area, zooplankton density will not be correlated to right whale call rate.*

My research focuses on North Atlantic right whale activity in CCB from January through May, where approximately one quarter of the right whale population is found during this time {Urazghildiiev, 2007 #282; C. W. Clark, 2007 #282}. In order to complete this research project, I have been granted access to two rich data sets:

acoustic data collected by the Cornell University Bioacoustics Research Program (BRP), the program in which I am a student; and zooplankton data collected by the Provincetown Center for Coastal Studies (PCCS). The results from the models run during the project's analyses support the alternative hypothesis that North Atlantic right whales do not acoustically advertise food resources. However, some of the models demonstrated that year has an effect on call numbers when only 2003 and 2006 are compared, suggesting that year may be indirectly related to zooplankton density.

BIOGRAPHICAL SKETCH

Ingrid Biedron was raised in Chelsea, Michigan. She studied at the University of Michigan before transferring to Dartmouth College to complete her Bachelor of Arts degree in 2003.

This thesis is dedicated to Dad, Mom, Caitlin and Griffin, who have encouraged my interest in marine biology since I was a young girl, and to Chris, who has been here with me in Ithaca during my graduate studies, offering enduring and appreciated support and advocacy.

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BRP Bioacoustics Research Program

CCB Cape Cod Bay

MARU Marine Autonomous Recording Unit

PPCS Provincetown Center for Coastal Studies

Chapter 1: Introduction - Communication, Acoustics, Mysticete Life History, and Hypotheses

Animal communication

Many species use acoustics for communication including whales, birds, elephants, frogs, primates, and insects (Payne 1971; Narins and Capranica 1978; Poole, Payne et al. 1988; Brown 1991; Hauser 1993a; Hauser 1993b; Hoy 2002). Species use acoustics to communicate information related to courtship, territory defense, resource advertisement, predators, and care for young (Bradbury 1998). Most authors agree that the definition of communication involves the transfer of information from a sender to a receiver, and that the receiver uses the information in determining how to respond. Bradbury and Vehrencamp (1998) use the definition "Communication is the provision of information that can be utilized by a receiver to make a decision." The signal is the avenue that delivers the information (Bradbury 1998) and is used by the sender to convince the receiver to take an action that will benefit both (Bradbury 1998).

"True communication" (Marler 1977; Markl 1985; Dusenbery 1992) occurs when, on average, both the sender and receiver benefit from the transmission of information. Consequently, evolution supports the development of signals by the sender that are successfully received and decoded by receiver and the refinement receiver's abilities to detect and decode signals. Communication will be optimized when the signal used to transfer information maximizes the difference between benefits and cost for the relevant context (Bradbury 1998). As the distance between a sender and receiver increases, it is more likely that receiver decision-making depends primarily on signals in lieu of tactical clues (Bradbury 1998).

The types of information animals convey to each other using communication include identity, status, activity, and environmental information (Bradbury 1998). The

amount of information exchanged and the costs associated with communication for both the sender and receiver vary depending on the context of communication. Costs include energy utilized, time, increased predator risk, and investment in physical structures (Bradbury 1998). Signals are adaptations that help animals survive in their environments. Therefore, natural selection must account for ambient noise, predator eavesdropping, and transmission efficiency and effectiveness (Bradbury 1998).

Sound characteristics

Sound speed in water is approximately 1450-1550 m/s depending on depth, temperature, and salinity (Sverdup 1970; Urick 1983). The defining characteristics of an acoustic signal are frequency, duration and energy level. Signal characteristics along these dimensions are often displayed using: a spectrogram, which plots frequency content as a function of intensity and time; a power spectrum, which plots sound energy as a function of frequency; and/or a frequency spectrum, which plots sound intensity as a function of frequency. A widely-used method to measure sound energy propagation in water is sound pressure, which is defined as the sound pressure level (SPL): SPL (dB) = 20 log (P/P(o)). P(o) is a standardized reference pressure (1 micro Pascal of pressure underwater). Decibels are units measured on a logarithmic scale to compare sound pressure levels as a ratio of measured sound pressure relative to the reference sound pressure (Sverdup 1970; Urick 1983).

Sound is transmitted via molecules in a medium. An event initiates the formation of a concentration of molecules. The molecules eventually return to their starting points. At each collision, the disturbance in molecules results in some disturbance energy being lost as heat. The second layer responds the same as the first, expanding, contacting neighbors, and retracting. Molecules that are condensed expand and contact the layer of molecules surrounding them. The wave of disturbance

collisions continues until all the energy created by the disturbance event has been dissipated as heat, at which point the sound will no longer be audible (Bradbury 1998). Sound waves can be transverse, perpendicular to the direction of wave propagation, or longitudinal. Sounds in liquids and gas are composed of longitudinal waves (Bradbury 1998). The frequency (f) of a sound wave is the number of times the wave cycles per unit time. Frequency is often measured in Hertz (Hz). One Hz equals 1 cycle per second. The wavelength (λ) of a sound is the distance between wave peaks. The speed of propagation of a sound (c) is equal to $f * \lambda$. As a sound travels outwards from its source, its intensity decreases, as a result of spreading loss (Bradbury 1998). Sound intensity decreases as the distance from the sound and its source increases. Other factors affecting the transmission of sound intensity include medium absorption, reflective scattering, and interactive scattering (Bradbury 1998).

The two accepted versions of sound propagation are spherical spreading and cylindrical spreading. Spherical spreading in the marine environment occurs when the distance of a sound from its source is less than or equal to the water depth. Spreading is cylindrical when the distance of a sound from its source is greater than water depth. The temperature and density of the medium through which a sound travels, as well as the speed and direction of wind and currents in the environment can cause refraction of sounds. As height in the air increases, or depth in water increases, sound propagation increases. At low altitudes (in air) and shallow depths (water), attenuation of sound, called a sound shadow, occurs (Bradbury 1998). At significant depths, variance in water temperature and pressure greatly affect sound velocity, which causes sound to refract from the surface and/or seafloor. When these refraction situations occur, low-frequency sounds enter a sound channel. In a sound channel, most sound travels within a certain range of depths and refraction and low absorption

result in low transmission loss and therefore huge ranges for acoustic communication (Clark 1983; Urick 1983; Jensen 1994).

Animal acoustics

Body size, signal contour, environmental medium, and substrate influence communication range (Bradbury 1998). The amplitude of a sound decreases dramatically when wavelengths are longer than the animal's body length. Due to their large size, whales produce sounds that are both low in frequency and high in amplitude, characteristics of signals used for long-distance communication. SNR for low intensity sounds will fall below the detection threshold (DT) at a shorter distance from the sound source than for high-frequency sounds. Therefore, acoustic environments and frequency ranges occupied by ambient noise will affect the optimal frequency range for communication signals. In shallow waters between 100 and 300 meters in depth, frequencies within the 100 - 400 Hz band have the lowest levels of transmission loss. Coastal cetacean species, including North Atlantic right whales (*Eubalaena glacialis)*, do exhibit higher frequency vocalizations than offshore cetaceans, illustrating this preference.

The ability to detect acoustic signals evolves within the limits of contextual constraints. For an animal to hear a sound as it is transmitted through a medium, that sound must be conveyed from the medium to the animal. The sound must then be captured, improved, and detected by the ear. Sound capture could be achieved using a particle detector, pressure detector, or pressure-differential detector. Cetaceans use a pressure detector, which includes a tympanum spread over a cavity that bends when far field sound pressures that are outside the tympanum are different from those inside the membrane (Bradbury 1998). To determine the direction from which a call is

produced using a pressure detector, the animal must have two detectors to compare the intensities, relative phases, or times of arrival of incoming sounds (Bradbury 1998).

To improve listening structures, animals most often evolve adaptations to increase the similarity between the medium and ear to decrease sound energy reflection. However, for animals in a marine or aquatic environment, the similarities between the impedance of the water and their ears are too similar and therefore they require areas of their body that have an impedance different enough from the medium that they move independently when receiving sounds (Bradbury 1998).

Animal communication is used to answer different questions in varying situations. Questions that could possibly be answered by communication using signals include: sender identity (individual, species, sex, age class); sender location (distance, bearing) relative to the receiver; and context (conflict resolution, territory defense, sexual interactions, parent-offspring interactions, social integration/coordination, and environmental contexts) (Bradbury 1998). For my research I will be focusing on questions about food signaling by North Atlantic right whales. Food signals convey information about the availability of food resources that can be shared (Bradbury 1998).

Coding is the linkage of alternative signals onto alternative conditions. The strength of the link between signal S_j and C_i is represented by a conditional probability: $P(S_j/C_i)$ (Bradbury 1998). The extent of coding depends on the number of alternative signals an animal produces. Coding is less extravagant in systems for which the signal set is constrained to a few stereotyped signal forms, which describes the apparently simple coding for right whales. There are three consistently repeated signal types in the species' repertoire: up calls, gunshots, and screams. As predicted, each of these signal types is seen in various contexts, suggesting that each signal codes for multiple conditions. Right whales may exhibit contextual coding, especially with

the use of up calls. Contextual coding occurs when the sender transmits an identical signal in different contexts, thereby requiring the receiver to determine the proper context, and therefore, appropriate meaning, of the signal (Bradbury 1998). Right whales of both sexes, all ages, and in all known habitats use the up call. When used in Cape Cod Bay (CCB), a feeding habitat, the up call may be a food recruitment call, whereas it may serve other purposes in the calving/wintering grounds or during migration.

Since coding and decoding costs increase as the number of alternative decisions increases, if questions have a limited number of simple answers, such as binary questions, which can only have two answers, costs are reduced. In feeding contexts, the relevant question is binary, "Are you feeding in your current location?" Therefore, the number of signal alternatives is minimal. If a right whale hears an up call in a feeding context, that may mean the sender is feeding on a zooplankton resource, and since the animal is feeding, that means that a preferred zooplankton species is available and the resource density is at or above the density at which the energy gained from feeding exceeds the costs associated with feeding. Therefore, if a receiver hears an up call in a feeding context, the whale can choose whether or not to move in the direction of the call and presumably toward the food resource. Repertoire size is the number of different signal types a sender transmits or a receiver can recognize (Bradbury 1998).

Optimality theory

Optimum signal accuracy and sensitivity allow for a certain amount of error that maximizes the benefits and minimizes the costs of signal production. The optimal sampling, or signaling, number maximizes the probability of detection without allowing it to be surpassed by signaling costs (Bradbury 1998). Right whales embody

this rule by producing signals over a period of time, but not signaling continuously. Signal detection is affected by detection ability in noisy environments, discriminating between signal types and classifying signals (Bradbury 1998). Compound signals contain information regarding more than one question and could transfer information about identity, location, and context simultaneously (Bradbury 1998).

Optimality theory seeks to explain the reasons certain communication systems and signals have evolved. Animals use optimality methods when deciding whether or not to communicate. Communication is defined as, "The transfer of information from a sender to a receiver that results in a change in the probability that the receiver will then elect an optimal action from a set of alternatives" (Bradbury 1998). Optimization is defined as, "The process of adjusting tradeoff variables to maximize or minimize some consequence," (Bradbury 1998). The probability that a receiver will choose an optimal strategy depends on the amount of information communicated and how the receivers make decisions.

Information value is determined by the increase in payoff with communication compared to the payoff without communication. The consequences that are maximized or minimized are measured in currency. For the purposes of animal communication, fitness is the unit of currency. Fitness is the abundances of certain genes throughout time. Often, individual reproductive success can be used as a proxy for fitness because it predicts the copying and propagation of an individual's genes. Reproductive success can be used as a predictor of fitness if the population size and age composition are stable, and the population is not vulnerable to density-dependent selection. Given these assumptions, the fitness estimated for different tradeoffs can be observed using individual lifetime fitness calculated for individuals accepting certain tradeoffs. Individual lifetime fitness is the survival (years of life) multiplied by its fecundity (number of offspring produced per year) (Bradbury 1998).

To reap the benefits of a tradeoff, an animal must conduct a strategy. A payoff is the amount of currency resulting from using a specific strategy. Mean payoff is calculated by determining the fitness for the strategy and accounting for the probability of the preferred outcome. Discounted fitness for each strategy is summed if there is more than one outcome per strategy. For any context, there will be choices between which strategies can be selected (Bradbury 1998). For example, a right whale, upon hearing an up call during April in CCB, can choose to swim in the direction of the call, or it can choose to not swim towards the call. The different options are called alternative strategies. Each strategy should be assigned a payoff, in terms of the currency, in our context, fitness or reproductive output. The optimization criterion, in the case in which fitness is the currency, is the criterion that maximizes fitness, or the strategy that gives the highest fitness.

Strategies can be defined as discrete, offering definite alternatives, or as continuous, offering a range of options in a specific sequence. The strategies for right whales responding to signaling of food resources are discrete: move toward the call or do not move toward the call. To determine the payoffs for a discrete strategy, the mean payoff for each strategy is calculated, and the strategy that results in the maximum or minimum amount of currency, is optimal. In a situation using fitness as currency, the optimal sequence would maximize fitness. To determine payoffs for continuous strategies, an equation must be created to link mean payoffs to the strategy and use calculus to solve the equation (Bradbury, 1998).

Mate attraction signals include information about identity (in right whales, species identity, not individual identity) and location, so the signals can have any contour, as long as it maximizes the transmission distance and receiver detection ability (Bradbury 1998). Right whale vocalizations recorded in CCB demonstrate traits characteristic of mate-attraction signals, including long-range transmission,

ability of the receiver to locate the sender, and ability to determine species identity (Bradbury 1998). Right whales maximize their communication success by producing the up call most commonly in CCB. Up calls are stereotypical calls with a low-frequency component that travel efficiently in the shallow CCB environment. Furthermore, right whales signal often, increasing the probability that they will be detected by conspecifics and evoke the optimal response.

For many species, courtship calls are produced only by males calling to females at short range, and individual identification is common (Bradbury 1998). However, studies have not yet demonstrated that right whales are individually identifiable by calls. Consequently, excluding calls coming from occasional surface active groups (SAGs) in CCB, the up calls commonly recorded in CCB are probably not functioning in courtship displays.

Territorial defense signals are individually identifiable and broadcasted over large distances. To be effective, receivers must be able to determine species and individual identification of the sender. Again, since studies have not demonstrated that right whales have individual voices, we cannot declare that territorial defense a function of right whale calling in CCB.

Acoustic sounds often last only a few seconds, so to communicate effectively, animals will usually have to repeat signals, which takes time, energy, and could attract eavesdroppers (Bradbury 1998). Since the costs of producing sounds and predator risks for right whales are relatively low, and eavesdropping is not a significant concern, repetition of signals is not prohibitively costly.

Game theory

I will rely on evolutionary game theory to support the hypothesis that North Atlantic right whales exhibit reciprocal sharing by cooperators. This technique

determines the optimal scenario in situations in which individuals can choose from multiple strategies (Bradbury 1998). The evolutionary game theory approach to explaining animal behavior is a big picture, long-term approach that makes predictions for how organisms in certain roles will respond rather than how individuals will respond. When using this approach, sections of the population that are expected to respond differently are assigned roles. This theory assumes that as a role evolves, it will favor one strategy. The opponent's strategy selection will be influenced by the evolution of the first animal's strategy, and the opponent may evolve to change his/her strategy, which in turn will affect that of the first role player. This constant evolution of strategies is called evolutionary game theory.

An evolutionarily stable strategy (ESS) is a strategy, or several strategies, that when it/they occur(s) often enough, cannot be displaced by other strategies from the same set of alternatives (Bradbury 1998). Evolutionary games are based on pure (single) strategies that are discrete (countable) or continuous (infinite possibilities) (Bradbury 1998). When the payoffs of a game depend only on the two players and do not depend on the number of other individuals choosing certain strategies, the game is called a contest. When the payoffs do depend on the numbers other of players choosing certain strategies, the game is called a scramble or referred to as "playing the field" (Bradbury 1998). In CCB, right whales participate in a give game, which is a discrete (swim towards call, do not swim towards call), symmetric (each player has access to the same strategies, the probabilities of either player winning are the same, and winning bestows equal payoffs), scramble (Bradbury 1998).

Cooperation

Cooperation is a product of the evolution of social behavior (Tyack 1983; de Waal 2003). Research shows that in societies in which many individuals participate in

cooperative foraging, all individuals receive an abundance of food (Kaplan 2000). If a communication system is cooperative, what kinds of signals have evolved to maximize fitness both for the sender and the receiver? (Bradbury 1998). The reciprocal sharing by cooperators that right whales demonstrate is a give game. Give games have two alternative ESSs: both players are reciprocal cooperators or neither player shares.

A give game is a situation in which the two strategies are to play donor or receiver. The donors give B fitness units to the receiver at a cost of C to themselves. Passives take donations from the donors but never give themselves. For donors to receive net benefits B must be greater than C and they must donate some days and receive donations other days. For a donor strategy ESS to evolve, donors must be able to discriminate between other donors and passives, and donate fewer benefits to passives (Bradbury 1998).

The assumptions for the payoff matrix in the figure below are:

1. $B>C$
2. When two passives meet, the payoff is P.
3. When donors meet, half of the time one is a donor and gives the other B at a cost of C, and vice versa.
4. When a donor interacts with a passive, half of the time the donor waits for a donation from the passive, and half of the time the donor gives the passive a discounted benefit b at cost k, or, the donor only gives to a fraction q of passives, where $0<q<1$, $b<B$, and $k<C$. In summary, donors give passives fewer benefits than donors give to donors.

If (B-C) < b than the passive strategy is a pure ESS. If (B-C) > b than there are two ESSs. There will be a pure ESS for the donor strategy and a pure ESS for the passive strategy (Bradbury 1998).

Give games are a model for reciprocal cooperation, in which one animal benefits another individual in the present and is compensated in the future (Bradbury 1998). However, evolutionary theory predicts that reciprocal cooperation happens infrequently: reciprocal cooperation is one of two ESSs that are both likely and occurs only when (B-C) is large (Trivers 1971).

At maximum, there are two alternative ESSs for the give game: cooperation and non-cooperation (Axelrod 1981). Cooperation is never a pure ESS when the presence of passive or selfish players is possible (Bradbury 1998). The give game can also be referred to as a scramble, since more than one receiver will hear the signals produced by sender. The evolution of reciprocal cooperation happens rarely, and in the case of right whales, it results from both the sender and the receiver benefiting relatively soon after the signal is sent (Bradbury 1998). Reciprocal cooperation is also more likely if kin selection results from the process and participating in reciprocal cooperation will benefit and propagate the genes of the donor (Bradbury 1998).

Table 1 Payoff matrix for the give game (Bradbury 1998).

		Opponent Plays	
Focal player plays		PASSIVE	DONOR
	PASSIVE	P	P+1/2b
	DONOR	P-1/2k	P+1/2(B-C)

Table 2 If B<C, and b≥0, then passive is a pure ESS (Bradbury 1998).

	PASSIVE	DONOR
PASSIVE	●	●
DONOR		

Table 3 If B>C and (B-C)>b, then there are two possible ESSs: always play passive or always play donor. Which is seen depends upon initial conditions (Bradbury 1998).

	PASSIVE	DONOR
PASSIVE	●	
DONOR		●

A donor animal may accept tradeoffs that limits its lifetime fitness but boosts the lifetime fitness of its relatives. Inclusive fitness occurs when increases in the number of genes in relatives are greater than the reduction in personal lifetime fitness. Individual selection will occur in situations in which individual fitness is a more accurate predictor of gene abundance; kin selection will occur in instances in which inclusive fitness is a better predictor of gene propagation (Bradbury 1998).

Vampire bats exhibit reciprocal cooperation. Vampire bats must feed at least every other day or they will starve. Female vampire bats will form partnerships with each other. If a bat does not find a meal one night, it will beg for food from its partner. In this case, B>C, the benefit of the sender (beggar) not dying is greater than the cost of the receiver donating a portion of its meal (Wilkinson 1984).

Zooplankton patches are constant over the duration of one to several days (Osterberg 2007). Therefore, even if a right whale acoustic signal originates from a sender several to tens of kilometers away and it takes several hours for the receiver to travel the distance to the sender, there is a high probability the resource will still be available when the receiver arrives. Once the zooplankton density threshold has been reached, there should be enough of the resource to share. Studies show that the temporal and spatial distribution of a zooplankton patch can stay constant despite right whales feeding within it (Baumgartner, Cole et al. 2003). Furthermore, the resource is ephemeral and patchy. Therefore, the animals will probably not exhaust the resource before it dissipates. However, the future time and location of available resources are uncertain and the discoverer of food in today's scenario, the sender, will most likely not discover the next food resource. Therefore, the sender of today will depend on other animals, potentially receivers benefiting from this discovery, to announce discovery of the next food resource. Due to the inconsistent and changing nature of the food resource, evolution favors reciprocal cooperation, or the "Give Game" (Bradbury 1998).

Environmental signaling

Scientists debate the use of environmental signaling between conspecifics and members of the same trophic level. Environmental signals can transmit information about the identity and/or presence of an object or resource, the resource's state, and/or the resource's location (Bradbury 1998). To most inexpensively advertise location, the sender broadcasts a signal at the time and location of object discovery, and the receivers travel in the direction of the signal. The main scientific question regarding environmental signals is how communicating information about the environment to

conspecifics benefits individuals. When a sender signals information about the environment, for example, information about a food resource, the sender pays the immediate time and signaling costs (necessary costs) and the receiver benefits relatively quickly. However, the sender will receive delayed benefits, and possibly even accrue additional costs, if additional animals attracted by advertising decrease the amount of resource available to the sender (incidental costs). Environmental signaling can be best justified when the sender receives large delayed, indirect, or mutual benefits, or the signaling benefits kin (Bradbury 1998).

The expected costs of signaling environmental information are minimal for right whales as sound production energy and time are relatively inexpensive in the ocean environment. Broadcasting signals is relatively cheap compared to other methods of communicating location, and the presence of eavesdroppers is unlikely, except for the potential humpback or fin whale that may diverge from its usual diet to feed on zooplankton (Bradbury 1998). Conspecifics are targeted receivers, and competition for the resource is unlikely due to the resource's nature. Zooplankton patches are not long-lived, so conspecifics attracted by food advertisement calls are not likely to deplete the food resource before it dissipates. Furthermore, perceived benefits, future notification and sharing of resources and potentially kin selection are high. If whales depend on individual discovery of zooplankton patches to sustain them, they may not find enough food to survive due to the patchy allocation of the resource. If individuals are truly reciprocally cooperative, then for each individual, the benefits of environmental signaling significantly outweigh the costs.

North Atlantic right whale signaling characteristics are representative of those expected from environmental signals, though possibly simpler. The signal form, generally upsweeps, may indicate the presence of food in the feeding context of CCB (this signal is used in all right whale habitats and may have different meanings

depending on context). The state of the food may not be indicated, although the fact that the animal sent the signal may indicate that zooplankton density is sufficient to make feeding worthwhile.

Due to the costs associated with higher numbers of signals for communicating larger amounts of information, environmental signals will most likely be simple and have one meaning. For example, a specific signal type will represent food in all contexts. Right whales seem to use the up call as the only food-related signal in CCB. All right whales, both males and females of all ages, use the up call in CCB (Clark 2007). Perhaps the up call represents different information in different habitats and/or behavioral contexts. For example, in CCB in the winter and spring months, the main information associated with an up call signal may be the advertisement of food resources.

Signals can be sent over the course of a day at a low rate with large inter-call intervals, allowing receivers to determine sender location. The receiver can use two ears to locate the sound and use the location and the amplitude of the call to estimate range. If the presence of up calls means food resources of sufficient density have been located by conspecifics, then the only decision receivers have to make is whether or not to swim toward the call, and by association, toward the food resource.

Environmental signaling of food or predator information between members of the same trophic level, or more specifically, to conspecifics, is believed to occur because of high benefits relative to costs as a result of reciprocal cooperation. Environmental signaling between animals at the same trophic level is rare. However, for the species that do demonstrate environmental signaling to members of the same trophic level, signaling costs are relatively low compared to the benefits gained from short-term direct benefits, indirect, deferred benefits, or the high degree of relatedness between senders and receivers (Bradbury 1998).

Resource-recruitment signaling

Resource-recruitment signaling, especially right whales signaling a food resource, is similar to environmental signaling. Resource-recruitment is the attraction of individuals to a resource by conspecifics, particularly, adults attracting adults. Cliff swallows (*Hirundo pyrrhonota*) practice resource-recruitment signaling (Brown 1991). Cliff swallows feed on swarms of insects. When an individual discovers a high quality swarm of insects on the feeding grounds, the individual sends a specific call to conspecifics. Like zooplankton, insect swarms are relatively large and shift often, so they are not defended and a single individual will not be able to exhaust the swarm before it moves on. Therefore, the sender does not experience incidental costs by sharing the resource. However, the sender will experience large short-term benefits as the swarm moves away from the location of sender discovery, and the reciprocal calling from senders notifies the initial sender of the location of the swarm as it moves or the location of a newly discovered swarm (Bradbury 1998). The zooplankton swarms that the right whales feed on are analogous to the insect swarms that the swallows feed on. Though reciprocal calling in right whales may take place over a longer time frame than the reciprocal calling of cliff swallows, the right whale resource-recruitment signaling can be thought of as tracking a single or multiple copepod patches as they aggregate and disperse throughout the bay. In this context, participating in reciprocal cooperation using resource-recruitment signals to advertise an ephemeral food source results in low costs and large direct relatively short-term benefits (Bradbury 1998).

Several primate species also exhibit food-recruitment calls. These species appear to use one signal for food discovery and another signal to transmit more detailed information about the resource. For example, spider monkeys (*Ateles geoffroyi*) sometimes whinny when a tree with fruit is discovered (Chapman 1990).

The probability and rate of whinnying increases as the size, divisibility, and density of the fruit patch increases. The whinnies are more likely to be sent by dominant individuals, which suggest that whinnies are given in situations in which recruiting conspecifics would be least costly (Bradbury 1998).

Several species of macaque monkeys (*Macaca*) signal food resource information. Toque macaques (*M. sinica*) produce a whee sound when large amounts of a food resource or a highly preferred food resource is discovered. Conspecifics immediately travel to the source of the call (Dittus 1984). Rhesus macaques (*M. mulatta*) send a signal when food is found and a different signal when it is eaten (Hauser 1993a; Hauser 1993b). Females signal more often as the number of kin in the vicinity increases. Signals for discovery are used when key foods are found, but they are also used in other contexts. This use of a signal for food in one context and to transmit different information in other contexts mirrors the hypothesis that right whales use the up call to advertise food resources in CCB although it may be used for separate purposes in other habitats.

Chimpanzees (*Pan troglodytes*) exhibit a food discovery call and a food consumption call (Marler 1977). The pan hoot is the food discovery call, and like the right whale up call, it is used in non-feeding contexts as well and is one of the most common calls for some populations within the species. Males pant hoot more often than females. The probability of pan hooting increases as the richness and preference for the food increases (Wrangham 1977; Ghiglieri 1984). Interestingly, for captive chimps, pant hoots were only made when large amounts of food were provided (Hauser 1987). The most calls were made when food was divisible and the amount was constant (Hauser 1993). Right whale food, zooplankton, is also easily divisible, and the relative amount available may remain constant if most patches disperse before they are depleted. Chimpanzees have been documented sharing food and

demonstrating reciprocity (de Waal 1989). Because groups of male chimpanzees are often related, kinship, may also explain why males make pant hoots most often.

Naked mole-rats (*Heterocephalus glaber*) have colonies with high genetic relatedness, and therefore, a social system reminiscent of social insects. Captive naked-mole rat worker individuals have been observed returning to the nest with discovered food and then vocalizing to other workers. The others then follow the advertiser's scent to the food source (Judd 1996). The high relatedness of the individuals in this species offsets the costs of announcing new food resources (Bradbury 1998).

Due to the costs of producing food-recruitment signals for vertebrates, when they do occur, they are simple, may allow discrimination between two food types at most, may denote quality but only on a large scale, and transfer location by sending a broadcast signal from the food discovery site (Bradbury 1998). Vertebrates (non-human) use resource-recruitment signals infrequently to provide simple information about resource characteristics. Location is advertised by broadcasting from the area in which resources are found (Bradbury 1998). Often, the species which use resource-recruitment signals do so to advertise relatively unlimited food sources for which there is little or no competition and/or for which the senders receive direct benefits or indirect benefits that outweigh sender costs (Bradbury 1998).

Sound transmission in marine environments

The sonar equation (Urick 1983) is used to describe acoustic propagation features. The source level (SL) is the acoustic output of the source and is measured in decibels (dB) (Clark 2002). As a sound travels outward from its source, the intensity decreases as a result of spreading loss, which can be spherical or cylindrical. Spherical spreading occurs until the radius from the source is the same as the water

depth, at which time cylindrical spreading takes place instead (Clark 2002). Absorption loss, due to the chemical properties of the water, also occurs. The directivity index (DI) is a measurement of binaural hearing (Au 1993). Transmission loss (TL) is defined as the combination of spreading and absorption losses. The received level (RL) is equal to the difference between SL and TL (Clark 2002).

Signal-to-noise ratio (SNR) is the ratio of the sound SL to spectrum noise level (NL) (Clark 2002). In order for a sound to be detected, the SNR must be greater than zero. The amount above zero at which a species can detect a sound is called the detection threshold (DT). The recognition threshold (RT) is the amount of SE needed to recognize a signal (Clark 2002). Signal excess (SE) is the difference between SNR and DT. SE must be a positive number to be detected or recognized. The definitions of SNR, SE, DT, and RT indicate that DT and RT will be greater if source level is higher, transmission loss is less, ambient noise is less, DI is greater, and DT is lower (Clark 2002). Changes to the physiological and neurophysiological adaptations would also improve DT and RT (Clark 2002). In order to increase detection and recognition, the transmission loss of the signal should be minimized and signal frequencies should be in the window with minimum TL and the bandwidths should be less than or equal to the minimum TL (Clark 2002). Bandwidth (W) is the difference between the lowest and highest frequencies of a sound (Clark 2002). The environment determines TL and NL. Therefore, selection will work on SL in order to decrease TL (Clark 2002). TL will decrease if absorption, and therefore frequency, decreases.

Empirical and modeled physical acoustic evidence shows that at distances of tens of kilometers, TL is roughly 10 dB less for sounds in the 100-500 Hz range than for sounds outside the 100-500 Hz bandwidth (Jensen 1994; Clark 2002). The main sources of shallow-water ambient noise are wind, waves breaking on the shore, seafloor substrate and biological sounds (Urick 1983; Wille and Geyer 1984; Clark

2002). Empirical evidence suggests that the frequency range of lowest ambient noise is from 100-400 Hz (Clark 1983).

Evolution of whale acoustic communication

Right whale signals have evolved for maximal transmission in relatively shallow, coastal, environments such as CCB. The range for right whale signals is less than that of offshore species that produce stereotyped, low frequency signals. For each context, there should be an optimal amount of information communicated, which is less than the amount that provides the receiver with complete certainty regarding the choice of optimal strategy. The amount of information transmitted is constrained by the costs of signaling (Bradbury 1998). As the amount of information transmitted increases, the probability of the receiver choosing the optimal strategy and the costs of signaling for both the sender and receiver also increase (Bradbury 1998).

Studies indicate that the right whale up call is used as a contact call to notify conspecifics of sender location (Clark 1980
). Up calls demonstrate the features of a signal that has evolved for long-range communication in a shallow-water habitat, with a spectral peak in the 100-200 Hz range where transmission loss and ambient noise are minimal (Clark 2000). Up call source level is the greatest of all right whale call types (Clark 2000). Due to evidence demonstrating frequency ranges of maximum transmission loss and minimum ambient noise, natural selection should have supported the evolution of sounds within the frequency range of 100-500 Hz.

Different signals address different questions. Signals used to address the same question are part of a signal set (Bradbury 1998). The total number of signal types used by senders or receivers is the signal repertoire size. In CCB, right whales have

demonstrated three types of signals: gunshots, scream calls, and up calls. Each of these signal types is part of the same repertoire.

Signal evolution is comprised of five steps: association between cue and condition, perception of the cue by the receiver, encoding rule linking the cue and condition, creation of the decision rule by the receiver, and receiver response (Bradbury 1998). If the response results in receiver benefit, the receiver will improve the perception, encoding rule, decision rule, and response. If the response is beneficial to the sender, the cue will become a true signal through ritualization. Simplification, exaggeration, repetition, and stereotypy lead to ritualization, which will increase the transfer of information (Bradbury 1998).

During acoustic communication, both the receivers and the senders experience costs (necessary costs and incidental costs) and constraints (Bradbury 1998). Senders deal with more constraints than receivers, because the evolution of structures to transmit signals are less likely to preexist for other purposes than structures which receive signals that may have already been present to detect predators and/or prey (Bradbury 1998).

Acoustic communication is limited more by the costs of signal production rather than receivers' abilities. Receivers demonstrate evolution of abilities for their ears to detect, localize, and process the signals sent by members of their species. Body size is one constraint on the signal amplitude and frequency produced by an animal. Sound production is constrained by body size because the bigger the body the lower the minimal frequency that can be produced by the animal. Due to their lengths, whales are able to produce sounds that are high in amplitude and low in frequency in comparison to other animals. High amplitude and low frequency signals are characteristic of long-distance communication (Bradbury 1998). For many species, sound production is energetically taxing (Bradbury 1998). Furthermore, the

large size of the right whale allows it to produce sounds that are low in frequency and high in intensity that can travel distances of at least tens of kilometers, a range that is comparable to the size of their CCB feeding habitat. Whales broadcast their sounds through water, which increases the range, and therefore, detection probability of the signals by receivers (Bradbury 1998)

The physical and energetic costs to right whales of sending acoustic signals is unknown, but assumed to be small for this large animal. North Atlantic right whales do not have predators other than humans and the occasional shark and killer whale, and therefore do not risk attracting predators with their signals. In some environments, the functional range of right whales may be smaller than the actual distance that calls are capable of traveling, at least in acoustic environments that have not been inundated by the noises of the industrial era. If the purpose of signaling in CCB is to announce a food resource, than the functional range would be equal to a distance that the receivers could travel before the resource dispersed.

In deep-water environments, evolution favors sounds that are lower in frequency than sounds in coastal habitats. In deep-water habitats, vocalizations can enter a sound channel in which sound travels efficiently at a certain depth that is determined by ocean temperature, pressure, latitude, and season (Urick 1983; Jensen 1994). Low-frequency sounds traveling in this sound channel are ideal for long-range communication (Clark 2002).

As expected, comparisons of deep-water species, for example, blues and fins, to shallow-water species, humpbacks and bowheads, indicate that the songs of pelagic species have smaller bandwidths and lower peak frequencies than those of coastal species (Clark 2002). Coastal species exhibit less stereotypy and redundancy than pelagic species, which affects detection and recognition, but have a wider bandwidth. A wider bandwidth suggests more complex communication and provides a measure of

range between senders and receivers of the same species. Because sounds of different frequencies are absorbed at different rates, some parts of a frequency-modulated call may reach a receiver, while other portions of the call do not. Based on the gaps in the call, the receiver, if familiar with the intact signal structure, can approximate sender range (Clark 2002). The cost of a larger frequency band is a shorter communication range. A deep-water signal that is low frequency and has a narrow bandwidth contains less information but has greater signal range than a coastal signal that has a higher-frequency and wider bandwidth (Clark 2002). To estimate hearing threshold, scientists assume that the lowest frequency of the hearing threshold is within the bandwidth of sound production and the frequency and frequency range at which the species' hearing is best can be estimated using comparisons to other marine mammals for which hearing thresholds have been measured (Clark 2002).

During the past fifty years, increases in anthropogenic sound in the oceans have decreased the area available for right whale communication in the United States to ten percent of its size one hundred years ago (Clark 2007). Increases in ambient noise due to human inputs may constrain communication ranges and flood the most effective frequency ranges for right whale acoustic signals. Scientists and managers are concerned that increases in ambient noise have reduced the listening and broadcasting range of right whales significantly enough to prevent individuals from locating enough food to maintain their optimal reproductive rates (Clark 2007).

Mysticete vocal communication

Currently, there are eleven extant species of baleen whales (Ridgway 1985). Mysticetes in the family *Balaenidae* include: the Bowhead whale (*Balaena mysticetus*), North Atlantic right whale (*Eubalaena glacialis*), Southern right whale (*Eubalaena australis*), and Pygmy right whale (*Caperea marginata*). Mysticetes in

the family *Balaenopteridae* include: the Blue whale (*Balaenoptera musculus*), Fin whale (*Balaenoptera physalus*), Sei whale (*Balaenoptera borealis*), Bryde's whale (*Balaenoptera edeni*), Minke whale (*Balaenoptera acutorostrata*), and Humpback whale (*Megaptera novaeangliae*). The family *Eschrichtiidae* includes one mysticete, the gray whale (*Eschrichtius robustus*)(Reeves, Mitchell et al. 1983).

Humpback whale sounds have been extensively studied for their vocalizations, including vocalizations related to feeding (D'Vincent 1985); breeding (Payne and McVay 1971; Tyack and Whitehead 1983); and male song (Winn and Winn 1978). Studies of Bowhead whale vocalizations suggest that they are used for navigation through sea ice, among other functions (Ellison 1986; George 1989).

Studies suggest that Blue whales use vocalizations to facilitate feeding, and/or migration and reproductive displays (Clark 1996; Clark 1997; Croll, Clark et al. 2001). Studies indicate that fin whale calls are used for male breeding displays calls (Croll, Clark et al. 2002). Sei and Minke sounds have not been extensively studied, and the functions of their calls have not been determined. South Atlantic right whale vocalizations, which have been thoroughly studied, are used for a variety of intra-specific interactions including social encounters, acoustic contact, and potentially resource advertisement (Payne 1971; Clark 1982; Clark 1983).

Through natural selection, baleen whales have passed the genes through generations for adaptations of traits that best promote survival. Internal (physiological, morphological, and phylogenic) and external factors (ecological, social, and physical environments) impact the amount of time it takes for traits to evolve (Clark 2002). For baleen whales, the physical environment largely determines which behavioral and morphological traits are selected throughout time (Clark 2002).

The first mysticete is assumed to have lived in coastal environments less than 40 m deep and to have eventually moved to deeper habitats in search of food along the

continental shelf and seamounts (Clark 2002). This assumption agrees with the molecular evidence showing that shallow-water right whales ancestrally predate the rorquals, which contain most offshore mysticete species (Messenger 1998). Right whales, together with bowheads, the other species in the *Balaenidae* family, are the least derived of the mysticetes. North Atlantic right whale vocalizations bear many of the same uses as Southern right whales including: courtship, resource advertisement, and contact calls (Clark 2007).

The characteristics of both coastal and pelagic mysticete sounds are well suited to their respective environments (Clark 2002). Signals for each habitat type match the frequency band that minimizes transmission loss and is lowest in ambient noise (Clark 2002). As is observed from the evolution of signal characteristics, ambient noise significantly affects the communication range of senders and receivers (Clark 2002). Therefore, the dramatic increases in ocean noise due to anthropogenic sources, especially ships, may dramatically reduce the communication range of mysticetes, and therefore the sharing of information necessary to survival.

The marine environment will exert pressures on the characteristics of baleen whale sounds. Due to the differences between shallow and deep-water environments, the acoustic characteristics of species using coastal and pelagic environments will evolve differently to maximize communication in each environment type (Clark 2002). The simpler calls seem to be associated with long-range signaling. Animals in surface active groups make complex calls that are frequency-modulated, amplitude-modulated, and broadband in frequency (Clark 2002).

The vocalizations of the Southern right whale have been extensively researched (Payne 1971; Cummings 1972; Saayman 1973), and associations between specific call types with behavior and activity levels have been made (Clark 1982; Clark 1983; Clark 1984). Early recordings of North Atlantic right whale vocalizations

were captured as low-frequency sounds of feeding right whales (Schevill 1962; Schevill 1962). Recent studies linking vocalizations and behavior of North Atlantic right whales demonstrate that southern right whales and North Atlantic right whales use the same types of sounds in the same contexts (Clark 2007).

North Atlantic right whale acoustics

Many species have evolved sounds with frequencies that minimize both transmission loss in their environment and ambient noise (Marten and Marler 1977; Wiley and Richards 1978; Clark 2004). The North Atlantic right whale call characteristics reflect these patterns (Urazghildiiev 2007). Most North Atlantic right whale sounds are tonal and have most energy below 1000 Hz. Some right whale sounds are stereotyped and relatively simple, and some are tonal and variable (Wright 2001; Parks 2003; Parks 2005; Parks, Hamilton et al. 2005). Right whales have three call types: up calls, tonal calls, and broadband calls. Up calls, often called contact calls, are most commonly used by North Atlantic right whale males, females, and juveniles. It is thought that they are used as contact calls to: inform conspecifics about the whereabouts of other animals; to maintain mother-calf contact; and to potentially advertise information regarding food resources. The up call is a low frequency call that begins around 50 Hz and increases to about 440 Hz and is one to two seconds in duration (Urazghildiiev 2007). The up call has been recorded in all known North Atlantic right whale habitats.

Tonal calls are often recorded from right whales in social groups called surface active groups (SAGs). SAGs are social groups in which there is often only one focal female, courted by several males. Sometimes juvenile whales or other females are present. SAG calls are often between 300 and 500 Hertz and are frequency and amplitude modulated. SAG calls are commonly recorded in the Bay of Fundy feeding

grounds. SAG vocalizations are occasionally recorded in CCB. SAG scream calls are made almost exclusively by adult females (Clark 2007).

Broadband sounds include gunshot sounds and sounds made by contact between water and a body part such as a flipper or fluke (Clark 2007). Gunshots are broadband sounds that sound like a loud crack and are produced internally by whales near the surface (Parks, Hamilton et al. 2005). Only male production of gunshot sounds has been confirmed. Broadband sounds are made during late summer and early fall and are thought to be a potential form of advertisement display to females (Parks, Hamilton et al. 2005).

Whaling and genetic diversity

North Atlantic right whales were first hunted more than a thousand years ago by the Basque shore-based fishery off the coasts of Spain and France. The North Atlantic right whale population, initially decimated by whaling, has been small for hundreds of years. As a result, the genetic diversity of North Atlantic right whales is limited: a factor that some scientists believe has contributed to the failure of the species to recover. Fortunately, research shows that some right whale pregnancies may fail because parental genetics are too similar, resulting in the genetic diversity for a population of this size being higher than expected (Kraus 2007).

Habitat use

North Atlantic right whales use several established habitat areas along the eastern coast of the United States and Canada. From approximately July to October, much of the population feeds in the Bay of Fundy. Some mothers never take their calves to the Bay of Fundy. These whales are called Non-Fundy whales (Rolland 2007). This phenomenon suggests that right whales have maternally directed site fidelity (Malik

1999). Therefore, if whales do not travel to the Bay of Fundy as calves, they may not gain the knowledge of the location of this summer feeding ground. In late fall, pregnant mothers, mothers with calves, and some juveniles, travel to the southeast United States, including South Carolina, Georgia, and Florida, where pregnant mothers give birth. The whereabouts of the right whales in the population that do not travel to the southeast United States during winter months, other than the whales that are found in CCB, are unknown during winter months. Based on the estimated twelve to thirteen month gestation period for right whales, mating is believed to occur during the winter, when a large percentage of the population is unaccounted for.

In the springtime, the animals in CCB are often observed moving southeast to the Great South Channel, where a large percentage of the population is found feeding from mid-May to June. Between early July and the start of August, many of the right whales return to the Bay of Fundy or Roseway Basin, an area 50 km south of Nova Scotia (Rolland 2007).

Critical habitat destruction could be one reason that the North Atlantic right whale population is not recovering as well as the South Atlantic population has recovered. However, the reduced calving rate (Kraus 2001) and the reduced use of feeding areas that were historically visited by right whales (Knowlton 2001) may indicate changes in food availability. The apparent correlation between feeding habitat usage and condition, calving rates, and population growth suggests an important relationship that must be considered when strategies are designed to protect North Atlantic right whales (Mayo 2001).

Surface active groups

Surface active groups (SAGs), are aggregations in which there are at least three animals, one of them a focal female, pursued by males. The behavior exhibited in

these groups may be practice for or actual mating (Kraus 2001; Best 2003). Females attract the males to SAGs with tonal calls (Parks 2003). Though sexual behavior is displayed during SAGs, in accordance with the gestation period of right whales and known calving season, it is highly likely that SAGs are social or practice events and fertilization events occur during the winter in unknown locations (Kraus 2007). Alternative explanations for the timing of SAG activity are that gestation may not be twelve months or delayed implantation of the egg occurs (Kraus 2007). Right whales do not appear to have long-term associations with conspecifics, except for mother/calf bonds. Tens of animals may participate in SAGs, but these associations last only several hours. Animals also aggregate while feeding, but these associations appear to dissolve after feeding ends. While participating in SAGs, right whales make all call types, blow, broadband, and tonal (Kraus 2007).

Population growth rates

The birth rate for the North Atlantic right whale species is low and the population contains a relatively high number of females that never calve (Kraus 2007). Right whales have a twelve to thirteen month gestation period (Best 1994). The only known calving area is the southeastern United States in coastal waters off Georgia and Florida, where the majority of calves are born from December through March (Kraus 2007). The mean calving interval from 1998 to 2003 was greater than five years, but in 2004 and 2005, calving intervals were only a little greater than three years (Kraus 2007). The mean age of first calving for the species is ten years (Kraus 2007).

Compared to the growth rate of the Southern right whale population, which is increasing at 6.9 to 7.1 percent each year (Best 2001; Cooke 2001) the North Atlantic right whale population grew at a 2.5 percent annual rate (Knowlton 1994) during the

1980s and had a negative population growth rate during the 1990s (Caswell, Fujiwara et al. 1999; Fujiwara 2001; Kraus, Brown et al. 2005).

There are multiple factors that may be preventing the North Atlantic population growth rate from improving. Scientists hypothesize that low genetic variability or inbreeding may be decreasing reproductive rate (Kraus 2007). Decreases in food resources could negatively affect female right whales' abilities to reproduce and lactate, resulting in reduced calving rates (Moore 2001). Reduced feeding could be caused by: a reduction in the number of copepods or a change in the conditions which cause them to aggregate (Baumgartner 2007); competition from other species, including Sei whales (Mitchell 1975); and/or hydrographic changes in the Gulf of Maine which affect copepod aggregation (Kenney 2001). Another explanation for slow/negative population growth rates may be that the North Atlantic right whale population is currently at carrying capacity. However, since historical levels of North Atlantic right whales were at least several thousand (Reeves 2007) and no oceanographic shifts of a matching magnitude have occurred since that time, it is unlikely that the species has reached carrying capacity (Baumgartner 2007). Anthropogenic causes of right whale death have unquestionably altered the population growth rate of the North Atlantic right whale, especially if contaminants have caused sterility. The right whale's food source is patchily distributed over space and time, which means that the right whale species' reproductive rates, which are dependent on resource availability, may mirror that pattern of abundance and paucity. The evolutionary strategy of animals with long life spans which live in variable environments is to survive the hard years and reproduce when times are good (Baumgartner 2007).

Though the historical population size of North Atlantic right whales is unknown (Aguilar 1986), the estimate of the original population size is at least 10,000.

Therefore, the current population size is significantly below carrying capacity, (if the availability of zooplankton and/or competitor threat has not changed in the last several hundred years). As a result, right whales should not experience intra-specific competition for food. However, correlations between worldwide atmospheric cycles and reproduction rates (Kenney 1998; Kenney 2001) and increased calving intervals concurrent with significant distributional shifts (Kraus 2001) imply that right whales are affected by changes in oceanographic conditions that affect prey availability (Kenney 2001).

Most likely, a combination of factors is responsible for the low population growth rates, including: low genetic diversity; reproductive failure caused by disease and pollutants; changes in caloric assimilation efficiency; and/or behavioral responses needed for mating or feeding (Kraus 2007). North Atlantic right whale reproduction is most likely linked to the availability of food resources and to human influences (Kraus 2007). If acoustics are used to advertise the presence of food and are therefore important to feeding success, then a better understanding of right whale acoustic communication while feeding is needed to facilitate this communication.

Feeding ecology

Currently, despite focused and long-term research on the North Atlantic right whale, the strategies, environmental cues, and sensory modalities that right whales use to migrate and forage are not well understood. The methods and strategies right whales use to find a feeding ground will be different than the methods used to locate a prey patch with optimal species and density (Kenney 2001). Although right whales aggregate on feeding grounds, studies have not yet strongly indicated that right whales communicate about the availability of food resources.

To feed, North Atlantic right whales filter zooplankton from the ocean water through two rows of baleen plates made of keratin (Pivorunas 1976; Mayo 2001). The whale swims with its mouth open and water enters the oral cavity via a break in the front of the mouth in between the rows of baleen plates. The whale pushes the water out of its mouth, but filaments in the plates catch prey of the correct size, which are larger than the spaces between the baleen (Mayo 2001). Experiments demonstrate that 95% of the available caloric content of zooplankton, mostly calanoid copepods, collected in areas where right whales were surface-feeding, was caught using 333 micrometer nets. These results suggest that the baleen's filtering efficiency focuses the right whale's feeding niche to a high energy, but spatially and temporally fleeting food source (Mayo 2001).

The primary prey of the North Atlantic right whale is *Calanus finmarchicus*, a calanoid copepod that is approximately 2 to 3 mm long. Right whales feed on *Calanus* in CCB (Mayo 1990), Great South Channel (Wishner 1988; Wishner, Schoenherr et al. 1995), lower Bay of Fundy (Murison and Gaskin 1989), and Roseway Basin (Baumgartner, Cole et al. 2003). North Atlantic right whales prefer later stage juveniles (copepodites) and adults at stage 5 of copepodites, or *C. finmarchicus*, C5 (Baumgartner 2007). Immediately before transitioning into an adult stage, copepods enter a dormant phase called diapause. When the copepods exit diapause, they move to the surface to feed on phytoplankton looming in early spring. Most *C. finmarchicus* are in diapause near the seafloor in summer and fall (Durbin 2000; Baumgartner, Cole et al. 2003; Baumgartner, Cole et al. 2003). While it is in its C5 stage, *C. finmarchicus* has a full oil sac filled with wax esters, which is up to half the zooplankton's size and makes a good calorie source (Miller, Crain et al. 2000). Though right whales prefer *C. finmarchicus* due to its rich caloric content and abundance in the North Atlantic, right whales also feed on *Pseudocalanus* and

Centropages typics (barnacle larvae) (Baumgartner 2007). On a few rare occasions, right whales have been observed feeding on young euphausiids (krill) (Collett 1909; Watkins and Schevill 1976).

Right whale feeding behavior is dependent on the life history phase of *C. finmarchicus*. Subsurface feeding is the most common feeding technique throughout all right whale habitats, and is most often seen in the lower Bay of Fundy and Roseway Basin, summer feeding habitats. The first generation of *C. finmarchicus* reaches its C5 stage in late winter or early spring (Baumgartner 2007), when right whales in CCB are known to feed on other copepod species (Mayo and Marx 1990). When C5 *C. finmarchicus* do appear in late winter, they are in the upper section of the water column in order to feed on phytoplankton in sunlight surface waters. As a result, right whales are seen surface feeding during this time. After phytoplankton abundance in CCB and Great South Channel (Mayo and Marx 1990) decreases in late spring, the majority of *C. finmarchicus* copepodites, many of them in stage C5, move into the deeper depths to enter diapause. Consequently, right whales complete long subsurface dives to feed on diapausing *C. finmarchicus* on the seafloor (Clark 2007). During the summer most *C. finmarchicus* are in diapause, when right whales are seen diving while feeding. During the *C. finmarchicus* movement from surface waters to depth, right whales have been observed in Great South Channel, in April through June, at the surface feeding and subsurface feeding (Baumgartner 2007).

The individual organisms that the right whales capture while swimming in their feeding paths are not mobile, so once the food has been engulfed and is within the mouth cavity of the right whale, filtering efficiency is the primary determinant of prey capture. Based on observations, right whales seem capable of determining if zooplankton density is high enough to continue feeding (Kenney 2001). In CCB, one of the right whale's regular feeding grounds during late winter and early spring, the

zooplankton community is largely composed of late stage calanoid copepods. Due to the right whale's filtering system, which targets larger zooplankton, and its inability to pursue fast-moving organisms, the right whale's trophic niche is an extremely energy-rich but constantly changing section of the marine food web. Therefore, right whale feeding is dependent on a particular type of zooplankton in a specific life stage that is spatially and temporally unpredictable (Mayo 2001). The ephemeral nature of the North Atlantic right whale's prey requires the whales to locate resource patches, even after they have reached the feeding grounds. Scientists do not fully understand how many species of cetaceans find food that occurs in patches tens of meters long or wide in areas of ocean tens of kilometers in length and width (Clark 2000). Except for mother-calf bonds (Taber 1982; Thomas 1984; Clark 2000), research has not provided evidence for social bonds between baleen whale individuals. However, while feeding, baleen whales do sometimes aggregate around prey patches, though evidence has not been gathered to suggest the advertisement of food resources (Clark 2000).

Research shows that right whale presence between patches of *Calanu*s does not necessarily depend on copepod biomass and *Calanus* abundance, which may indicate that right whales might target patches with copepods of older life stages. Chance may also play a part in right whale selection of target patch (Wishner, Schoenherr et al. 1995). However, some of the highest zooplankton density measurements have been collected near feeding right whales (Kenney, Hyman et al. 1986; Murison and Gaskin 1989; Mayo and Marx 1990; Mayo 1992; Macaulay 1995; Wishner, Schoenherr et al. 1995; Beardsley, Epstein et al. 1996; Kenney 2001). This fact raises the question, "How do right whales first find their feeding grounds and then find patches of zooplankton at or above their threshold feeding densities?"

Previous research documented low right whale vocalization rates while feeding (Watkins and Schevill 1976). However, recordings from CCB during the winter,

during times when feeding is one of the right whales' primary activities, suggest that acoustics might explain how right whales locate food. Clearly, additional research is needed to define how and if North Atlantic right whales use acoustics to communicate information regarding food resources.

Some scientists hypothesize that to locate food, North Atlantic right whales pay attention to environmental cues about water mass characteristics including water temperature, currents, salinity, stratification, and chemistry (Norris 1967). Others hypothesize that to find zooplankton patches once they have reached the general Gulf of Maine feeding grounds, whales detect sounds made by other predators preying on zooplankton such as fish and birds (Kenney 2001). Salinity, if indicative of environmental situations favorable to the development of thick copepod densities, or other chemosensory cues, such as organic compounds made by the zooplankton themselves, may help whales pinpoint areas of high copepod density (Kenney 2001). In order to detect chemicals in the water and localize a potential food source, right whales must be able to smell the chemicals and determine which direction the smell is coming from (Kenney 2001).

As mentioned before, right whales could potentially use temperature to find zooplankton patches. In Great South Channel, right whales have been found feeding on patches of copepods that are north of the tidal mixing area, in which there is a stratified, warmer surface layer water mass where the mixing is occurring (Brown 1989; Wishner, Schoenherr et al. 1995; Chen 1995b).

On the scale of 1 to 10 kilometers, right whales are often seen aggregated in numbers of several to tens of animals within an area only a few kilometers in radius or less (Kraus 1988; Murison and Gaskin 1989; Kenney, Winn et al. 1995). Sometimes, single right whales are observed outside the aggregations. Studies using right whale satellite tags have demonstrated that whales sometimes travel significant distances,

suggesting that they are searching for potential feeding areas (Mate, Nieukirk et al. 1997). In order for scouts to share knowledge of newly discovered feeding resources with conspecifics, right whales would potentially need to communicate this information over significant distances (Kenney 2001). Another explanation for these non-aggregated right whales is that they are competitors and/or younger animals that have not gained access to the resource (Hain 1995).

Scientists are unsure of how, at the micro scale, centimeters to tens of meters in length, right whales find optimally dense patches of zooplankton within the feeding grounds. Chemical cues may provide some assistance, but chemical cueing will depend on persistence, turbulence, diffusion, and dispersal rate. Tasting the water may help, but will accrue the costs of mouth opening and drag (Kenney 2001). Right whales observed feeding on cyprids in CCB terminate feeding behavior quickly after beginning, perhaps because the small size of cyprid individuals reduces filtering efficiency (Kenney 2001). At the micro scale, tactile cues are probably most effective. Right whales have vibrissae, or sinus hairs, in their heads, which they can use to detect individual zooplankton. The vibrissae are most dense near the front of the mouth opening. The vibrissae on whales are enervated and appear sensitive to touch (Ling 1977).

North Atlantic right whales swim at approximately 1.5 m/s while feeding (Hammer 1988; Werth 2004). Right whales are limited in their prey options by both their filtering efficiency and their slow swimming speed, which requires them to feed on slower organisms. Right whale feeding style is characterized by winding paths, apparently shadowing the densest, and therefore most calorie rich, sections of zooplankton patches. Sub-surface feeding occurs when right whales are still feeding in the upper portion of the water column, but remain submerged, assumedly feeding on the most calorie dense zooplankton layer. Right whales have also been observed

diving to feed on a zooplankton layer near the ocean floor. Right whales adjust their feeding behavior in response to zooplankton species type, density, and distribution. Right whales are slow swimmers, and therefore they cannot or do not swim fast enough to overcome the avoidance response of krill. Perhaps the increased cost of swimming faster would outweigh the benefit of capturing a richer food source (Kenney 2001). A feeding whale would ideally feed on zooplankton patches that provide the maximum net energy intake.

North Atlantic right whales have demonstrated that they require a maximum copepod density to be present before opening their mouths**.** The estimated threshold zooplankton density required for right whales to open their mouths to feed is approximately 4,000 individuals per cubic meter. The number of zooplankton individuals per cubic meter of water, not the size of the individual zooplankton, seems to influence feeding threshold (Mayo 1992). Right whales have evolved to capture late-stage *C. finmarchicus*, which are relatively large plankton that are rich in energy (Mayo 2001). Consequently, right whales may have a method of determining the type and associated density of zooplankton in their path, allowing them to approximate the energy available within the patch (Kenney 2001). Right whale feeding behavior suggests that right whales are able to make these determinations, both in the horizontal and vertical dimensions. Feeding right whales move in nonlinear paths, winding back and forth, assumedly following the densest path of copepods (Mayo and Marx 1990). Studies show that right whales that are surface feeding often change the depth at which they swim (Mayo 1992). Zooplankton samples collected in a right whale habitat show that if right whales change their vertical depth as little as 20 cm, their energy input could increase up to 20% (Mayo 1992).

During the day, right whales may be able to see their prey, or at least the thickness of the patch, at the surface while skim feeding. However, right whales

commonly feed in conditions with low light levels, where vision will not help determine the location and/or preferability of the food resources. These low light conditions include feeding at dawn, dusk, or nighttime and feeding at depth. Right whales feed at depth in the Great South Channel (Kenney, Winn et al. 1995; Winn, Goodyear et al. 1995) and Bay of Fundy (Murison and Gaskin 1989; Goodyear 1993). Bioluminescent species of copepods may be visible at night (*Metridia lucens*) (Kenney 2001).

Mortality and threats to survival

The North Atlantic right whale, a species numbering approximately 350 individuals, is one of the most endangered whales in the world (Clapham 1999). The species was initially decimated by whaling and has been unable to recover although hunting North Atlantic right whales has been prohibited for more than seven decades (Rolland 2007). North Atlantic right whales were historically whaled because they were the "right" whale to kill due to their slow swimming speed, rich oil content, and ability to float and be easily transported onto the whaling ship after being harpooned (Caswell, Fujiwara et al. 1999; Fujiwara 2001).

Today, ship strikes and entanglements in fishing gear are the main causes of North Atlantic right whale mortalities. If current rates of human-induced deaths persist, the species could be extinct within two hundred years. However, if the deaths of two females per year could be avoided, the population growth rate could level off, or even increase (Caswell, Fujiwara et al. 1999; Fujiwara 2001). In the last six years, at least nine right whales have been killed as a result of ship strikes, and four have been killed by entanglements (Moore 2007).

North Atlantic right whales are members of the order *Cetacea*, which includes whales, dolphins, and porpoises. Baleen whales are in the suborder Mysticeti. Right

whales, as well as bowhead whales, are in the family *Balaenidae* (Rolland 2007). There are three right whale species, *Eubalaena glacialis*, North Atlantic right whales, *Eubalaena australis*, southern Hemisphere right whales, and *Eubalaena japonica*, North Pacific right whales. Historically, *Eubalaena glacialis* occurred in both the western and eastern North Atlantic oceans. However, today, there may only be a handful of individuals remaining in the eastern North Atlantic (Rolland 2007). North Atlantic right whales presently range from Iceland to the Gulf of Mexico (Rolland 2007).

Adults are approximately 14 m long, with females about 1 m longer than males (Allen 1908; Andrews 1908) and weigh about 36,000-72,000 kg. They are large, wide whales, usually black, and they sometimes have white patches on the chin and stomach. Callosities, dark rough skin spots are found on the head and face. The callosities appear whitish because they are covered by *cyamid* crustaceans, or whale lice. Since the callosity pattern is different for each whale, photographs of callosities are used to identify individual whales (Hamilton 2007).

North Atlantic right whales had been hunted for approximately one thousand years before they were protected from whaling in 1935 by the League of Nations (Rolland 2007). Today the North Atlantic right whale is protected by stringent laws under the U.S. Endangered Species Act and the Marine Mammal Protection Act and by Fisheries and Oceans Canada (Rolland 2007). In the United States, CCB, Massachusetts Bay, the Great South Channel, and the coastal waters of the southeastern United States have been designated critical habitat areas by the United States National Marine Fisheries Service. Canada has established two conservation zones, the Bay of Fundy and Roseway Basin, on the Nova Scotian Shelf (Rolland 2007). A group of governmental and non-governmental organizations and individuals

have formed the "North Atlantic Right Whale Consortium" to study and share information and research to promote the protection of the North Atlantic right whale.

North Atlantic right whale vocalizations

North Atlantic right whale calls fall into three categories: blow sounds, broadband sounds and tonal sounds (Clark 2007). Blow sounds are noises made from exhalations. Some blow sounds produced in SAGs and social situations are greater in intensity than usual breathing exhalations (Wursig 1993). Broadband sounds come in two forms: non-vocal slaps, including flipper slapping, tail slapping, and breaching, and gunshots. Gunshots are loud cracking sounds that right whales make internally while near the ocean surface (Parks, Hamilton et al. 2005). The purpose of gunshot calls is undetermined. However, they are made primarily by males during late summer and early fall and are suspected of being related to mating or male-male agonistic interactions (Parks, Hamilton et al. 2005). The final call type is the tonal call, which comes in the form of low-frequency stereotyped vocalizations and complicated, frequency-modulated, calls of higher frequency. The low-frequency contact call, a simple signal one to two seconds in duration, is the most common vocalization made by right whales and is made by individuals of both sexes and all ages. Scientists believe that contact calls are used to maintain acoustic contact between animals. For example, contact calls may be used by: mothers attracting wandering calves; males entering SAGs, lone whales, and perhaps by whales locating conspecifics (Clark 2007). A frequency-modulated call, named the scream call, is a call type that includes vocalizations that are tonal, contain harmonics, and sounds like moans. Females that are the focus of SAGs make these sounds most often, though males are capable of making tonal sounds. Screams can waver in frequency or remain constant, and they can be less than a second or up to four seconds in duration. Other stereotypical calls

include down calls, sweeping from high to low frequency, and constant calls, with unchanging frequency (Clark 2007).

As a result of right whales relying heavily on sound as a sensory tool, the potential impacts of increased anthropogenic noise in the marine environment are significant. A decrease in the range of communication caused by increased ocean noise could reduce the ability of right whales to locate mates and food due to masking, an event during which right whale calls made in the presence of ships or other sources of noise are acoustically observed. Furthermore, noise could cause a chronic stress response causing short-term or permanent hearing loss, making it difficult for right whales to hear other whales or ships. Also, the cumulative effect of multiple stressors on right whales, including contaminants and food shortages, in addition to increases in noise, could lead to poor health and decreases in immune and reproductive system health (Evans 2003; Otten 2004; Clark 2007).

Impacts of ocean noise

Sources of anthropogenic noise in the ocean include shipping, construction, dredging, depth finders used for fishing and bottom mapping, and seismic oil exploration (Clark 2007). Low-frequency noise travels over large distances in the ocean, with some intense sources broadcasting around half the world (Munk 1994; Parks, Clark et al. 2007). Noise events, such as mid-frequency active naval sonar can have short-term effects, such as mass standings, on marine mammals (Frantzis 1998; Cox 2006; Parks, Clark et al. 2007). Ambient noise from ships can also cause short-term behavioral changes (Lesage 1999; Buckstaff 2004; Foote 2004; Scheifele 2005). However, the long-term effects of anthropogenic noise sources are not well studied (Parks, Clark et al. 2007). As the North Atlantic right whale population size

decreases, attempts to find conspecifics for mating, socializing, or to advertise food to, will become more difficult. Increases in ambient noise will decrease the range over which whales can communicate, making transfer of information even more difficult for whales (Parks, Clark et al. 2007).

The "soundscape" of the ocean includes environmental noise (wind, waves, and earthquakes), biological noise (fish, invertebrates, and marine mammals), and anthropogenic noise. Right whales have evolved to produce sounds that are in frequency ranges that do not overlap with ambient noise. Furthermore, their low frequency sounds minimize transmission loss (Clark 1983), thereby maximizing communication range. Unfortunately, shipping noise floods the range in which right whales hear and can potentially result in loss of right whale hearing and/or decrease their range of communication (Clark 2007). Today, commercial shipping is the primary marine sound source in the 5 – 200 Hz band (Payne and Webb 1971). Most noise from distant ships is below 100 Hz (Wenz 1962). Ambient noise resulting from long range shipping has increased most in the frequency range from 20 to 100 Hz (Ross 1974; Andrew 2002; McDonald 2006; Parks, Clark et al. 2007).

North Atlantic right whales are long-lived, with life spans of at least 65 years (Hamilton 1998). Due to their long life spans, increases in ambient noise in the oceans have outpaced the ability of right whales to evolve to cope with noise in their environments. Recent studies found that in environments with high levels of ambient noise, right whale calls have a higher average fundamental frequency and the whales call at a lower rate. This may be an attempt to avoid masking of whale calls by low-frequency shipping noise. Decreased call rates reduce the costs of calling, especially if increased call amplitudes are needed are needed to transmit a signal effectively in noisy environments. Right whales have made changes in call frequency and rate

within their lifetimes, demonstrating a change in behavior, not a result of natural selection (Parks, Clark et al. 2007).

To sufficiently comprehend the impacts of noise on right whale survival, scientists need to understand the range over which whales can communicate, or their directional range of communication. Masking is one result of high levels of noise. Masking occurs when the sound of interest is covered by other obstructing sounds, often of similar frequencies. Contact calls are used for counter-calling over at least 8 km on days with low levels of background noise (Clark 2007). If North Atlantic right whales were historically able to communicate at a range of 16 km, then the hearing area in which two animals may acoustically communicate has been reduced to 10% of its size hundred years ago. This means that the tiny North Atlantic right whale population of today has a significantly lower chance of finding mates and food, if food resources are advertised acoustically (Clark 2007).

Studies in terrestrial animals demonstrate that increases in environmental noise can precipitate a chronic stress response (Evans 2003; Otten 2004). Noise could be affecting right whales physically as well as neurologically. The noise levels throughout their habitat are great enough to cause short-term or permanent hearing loss, further decreasing their ability to detect approaching ships and/or communicate with conspecifics (Clark 2007). Better understanding how right whales use sound to communicate will provide insights into how anthropogenic noise impacts their feeding, migration, social interactions, and overall survival.

Research background

Dr. Charles Mayo, director of the Right Whale Habitat Studies Program at the Provincetown Center for Coastal Studies (PCCS), has conducted habitat assessment studies in CCB for two decades. Based on his long-term assessments of right whale

behavior and zooplankton abundance, distribution, and species composition in this critical right whale habitat, Dr. Mayo has determined that right whales use sensory information to locate food resources (Mayo 2007). Dr. Mayo's observation that right whales rely on a form of remote sensing to locate zooplankton aggregations inspired his collaboration with the Cornell Bioacoustics Research Program (BRP) to explore the relationship between plankton abundance and distribution and right whale acoustic behavior.

Currently the functional significance of right whales producing contact calls in the context of searching for food and feeding is not understood. Scientists assume that right whales do not share food and do not need other whales to obtain food (Baumgartner 2007). The research described in the following pages is directed at exploring and questioning these assumptions regarding the relationship between North Atlantic right whale acoustic and feeding behavior.

Technology

In the last 20 years, 19 North Atlantic right whales have been killed by ship strikes (Kraus, Brown et al. 2005). In recent years, passive acoustic technology has grown to be an increasingly effective and efficient method to determine the presence and seasonal distribution of whales, information that is important for the development of management strategies to protect North Atlantic right whales from human activities. In the past, visual aerial and shipboard surveys have been used to detect and report whale distribution information to ships. However, unlike visual surveys, which are limited by weather and time of day, acoustic surveys provide a continuous survey approach that reports right whale presence on a larger scale which is safer and less expensive. The probability of detecting a right whale acoustically is about 100 times more likely than detecting one visually from a boat or plane (Clark 2007). One

negative aspect of acoustic detection is that location accuracy is correct only to several hundred meters. Therefore animal number in a group is difficult to determine. Another difficulty with using passive acoustics is that anthropogenic noise can obscure right whale calls, which will go undetected (Urazghildiiev and Clark 2007; Urazghildiiev and Clark 2007)

Currently, the BRP, the program in which I am a student, uses a type of passive acoustic technology called a marine autonomous recording unit (MARU) to record biological sounds. Passive acoustic technology is used to detect and localize right whales. With this information, managers can determine the seasonal distribution of right whales, at least for the whales which are vocalizing, and identify the areas most heavily used by right whales (Clark 2007).

The acoustic data for the CCB right whale acoustics and feeding research project has been collected using MARUs. MARU contents include a microphone, amplifier, hard drive, software, and batteries enclosed in a glass sphere inside a yellow plastic covering (Clark 2002). While recording, MARUs rest on the seafloor, anchored by sandbags. MARUs deployed in CCB were arranged in an array, which means that they were placed closely together so that a vocalizing whale in the recording vicinity of any of the MARUs would hopefully be recorded on at least 3 units. Using time of arrival location methodology whales, that were detected by at least 3 MARUs could be assigned a geographical location (Clark 1996; Desharnais 2004). MARUs can be programmed to sample in the frequency range relevant for the target species, which for right whales is approximately 2 kHz.

After the MARUs are retrieved, the hard drive is removed and recordings are converted to sound files. Acoustic analysts measure the frequency, duration, and intensity of vocalizations. To view and analyze the recordings, spectrograms are used to plot the intensity, frequency, and time of the recordings. Instead of listening to

entire recordings to identify sounds of interest, analysts visually browse spectrograms, and then listen only to the recording sections that are of interest (Clark 2007).

Management applications for research

Previous studies (Matthews 2001; Vanderlaan, Hay et al. 2003) have demonstrated that right whales use sound to communicate in a variety of contexts including social activities, (Kraus 2001; Parks 2003), mother and calf interactions, and potentially male-male agonistic behavior (Clark 1983; Wursig 1993). However, right whale acoustic behavior in the context of feeding is poorly understood. In order to more effectively protect North Atlantic right whales, scientists must improve their knowledge of the acoustic communication on which these animals rely for survival.

If right whales do use sound to communicate with other whales regarding the location of food, increased ambient noise levels in the oceans would decrease their ability to hear other whales, and as a result, lower their abilities to locate food. Studies suggest that when mothers are underweight, calving intervals, the length of time between a mother's birthing events, are longer (Wade 1992; Kraus, Brown et al. 2005; Rolland 2007). Therefore, rising ambient ocean noise levels may be inhibiting whale communication and therefore mothers' abilities to feed and reproduce, which may lead to a decline in right whale population numbers (Baumgartner 2007; Clark 2007).

Understanding if and how right whales use acoustics to find food will help scientists and policy makers determine how to most effectively mitigate the effects of increasing levels of ambient noise on right whale population health. Furthermore, if the link between acoustics and feeding behavior is established, efforts to implement restrictions on anthropogenic inputs of sound into habitats critical to right whales will be more likely to succeed.

Hypotheses and predictions

The research focuses on the hypothesis:

- North Atlantic right whales acoustically advertise food resources, thereby practicing reciprocal cooperation.

The prediction following this hypothesis is:

- Within a given area, zooplankton density will be correlated to right whale call rate.

Alternative Hypothesis:

- North Atlantic right whales do not acoustically advertise food resources nor participate in reciprocal cooperation.

The prediction following the alternative is hypothesis is:

- Within a specific area, zooplankton density will not be correlated to right whale call rate.

Chapter 2: Methods, Results, and Discussion - the relationship between zooplankton density and North Atlantic right whale feeding behavior in Cape Cod Bay, Massachusetts

Methods

Data collection

My research focuses on North Atlantic right whale (*Eubalaena glacialis*) activity in Cape Cod Bay (CCB) from January through May, where approximately one quarter of the right whale population is found during this time (Clark 2007). CCB is an ideal research site because this habitat provides a manageable study area in which to simultaneously study right whale acoustic behavior and zooplankton availability. Furthermore, I have been granted access to two rich data sets, the acoustic data collected by the Cornell University Bioacoustics Research Program (BRP), the program in which I am a student, and the zooplankton data collected by the Provincetown Center for Coastal Studies (PCCS), for this research.

The PCCS, a collaborator and non-profit organization that conducts right whale habitat assessment studies in CCB, has agreed to provide access to its feeding ecology data for use during my research. On fair-weather days during the winter season, researchers from the PCCS travel to each of 4 quadrants in CCB to collect plankton samples. In each quadrant, samples are collected at 2 stations. To collect samples, researchers drag a plankton net horizontally through the water column to collect surface samples of zooplankton density and species composition (Osterberg 2007).

Researchers from the BRP collected the acoustic data I am using for my thesis. Between three and eight marine autonomous recording units (MARUs) were deployed in CCB at the beginning of the winter season in 2003, 2005, and 2006. The MARUs continuously recorded all biological, environmental, and anthropogenic sounds within a sampling rate between 2000 and 4000 Hz, a frequency range that includes all right

whale vocalizations (Clark 2002; C. W. Clark 2007). When the MARUs were retrieved from CCB and returned to the BRP, the hard drives were removed and given to acoustic analysts who used specialized software to extract the sound data from the hard drives, merge the sound data from the MARUs, and create digital sound files (Clark 1996; Desharnais 2004). I performed my acoustic analyses at the BRP, using software developed by BRP computer programmers that project the CCB recordings in spectrographic form and assign a bearing to call events recorded on 3 or more channels (Urazghildiiev and Clark 2007; Figueroa 2008).

Data analysis

To select the days that I included in my analysis, I first set the outer boundaries of the season from which I would select days. This season began April 1 and continued through May 5 for all years included in the analysis (2003, 2005, and 2006). During that time frame, I identified all days on which a zooplankton sample was collected and created a log of right whale calls for each of those days using a software program called XBAT (Urazghildiiev and Clark 2007; Figueroa 2008). I included all samples collected during the spring sampling time frame in my modeling of the effect of bay total zooplankton density on bay total overall right whale call rate.

Next, for all logs of calls, I used a software program called ISRAT_LT (Urazghildiiev and Clark 2007) to calculate and assign each call a bearing. If a call was not recorded on 3 or more of the recording units, it was deleted from the log. The reference point for bearing was the MARU that was the center of the array. Each call was assigned to a region based on its bearing: an event with a bearing of 0 to 90 degrees was assigned to Region 1; an event with a bearing of 90 to 180 degrees was assigned to Region 2; and an event with a bearing of 180 to 270 degrees was assigned to Region 3. Events with a bearing of 270 to 360 degrees were not assigned bearings

because the MARU deployment positions did not allow for accurate calculation of bearings in the geographical area that is represented by the 270 to 360 degree range.

After right whale calls were assigned to a region, the zooplankton sampling station most centrally located in each region was identified, and zooplankton densities from each region's designated station were used in the JMP statistical models to determine the effects of zooplankton density, day, year, and the interaction between zooplankton density and year on right whale calling behavior (Figures 1-5).

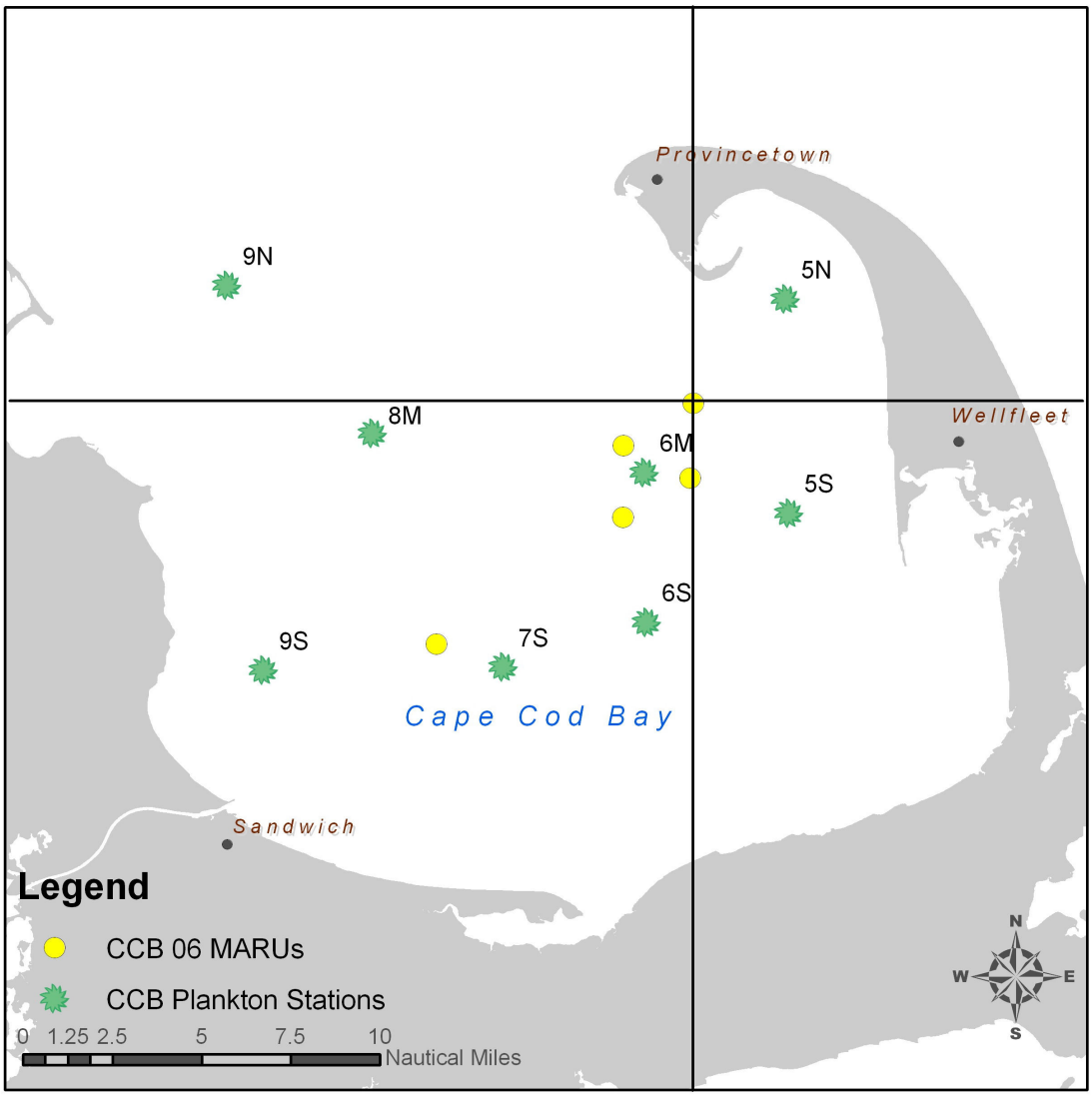

Figure 1 Cape Cod Bay MARU and plankton sampling stations for the CCB 06 deployment, during which acoustic data were recorded in 2003.

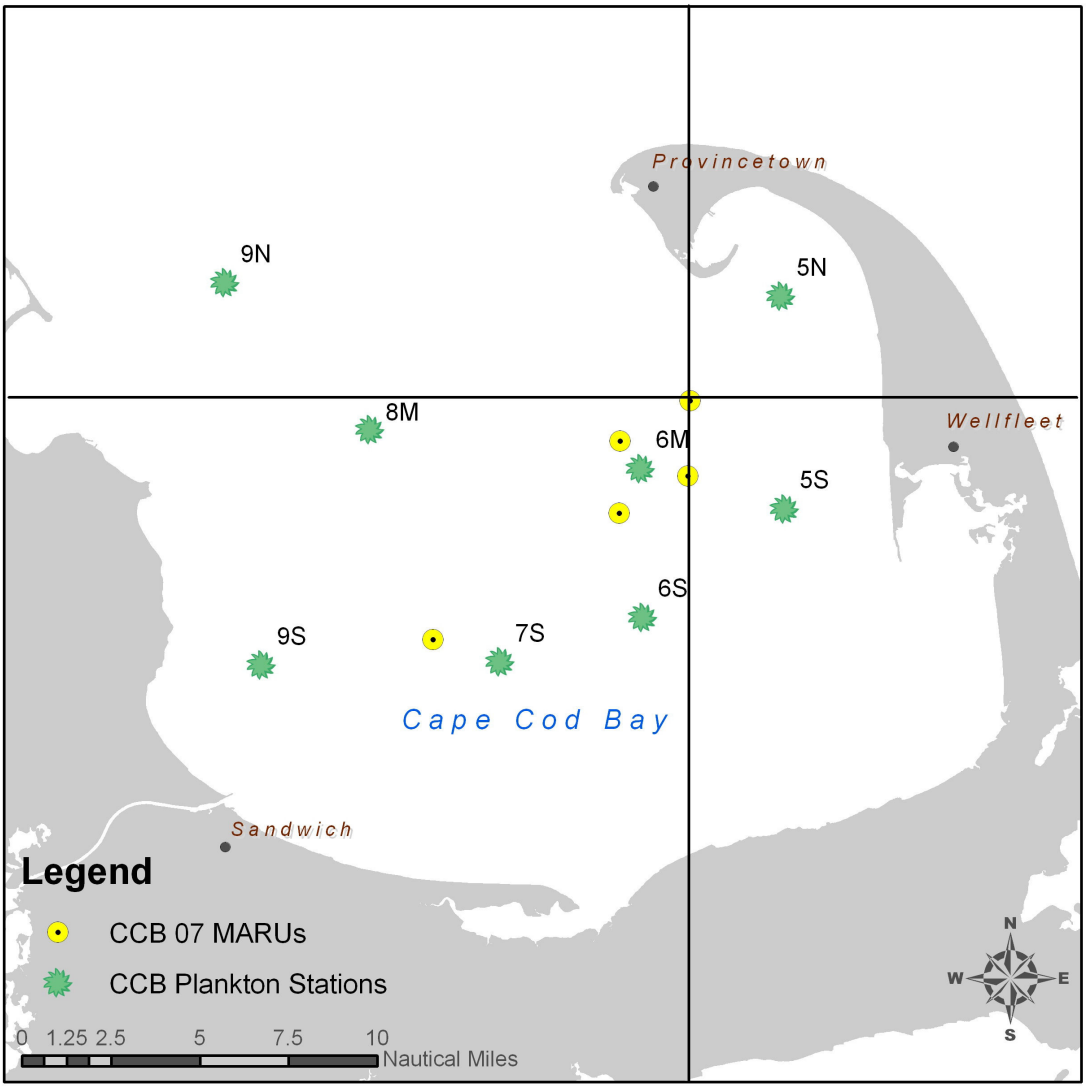

Figure 2 Cape Cod Bay MARU and plankton sampling stations for the CCB 07 deployment, during which acoustic data were recorded in 2003.

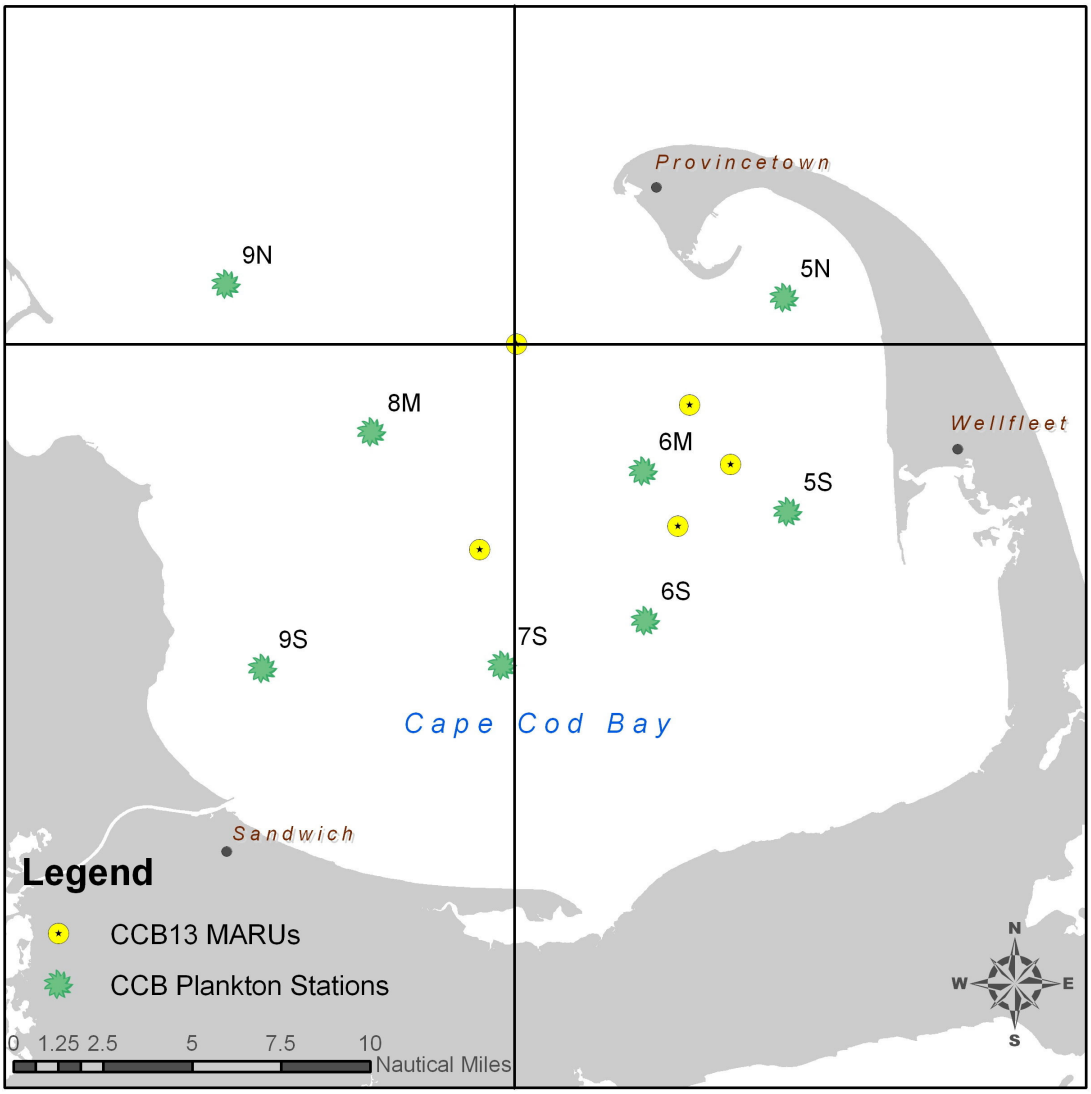

Figure 3 Cape Cod Bay MARU and plankton sampling stations for the CCB 13 deployment, during which acoustic data were recorded in 2005.

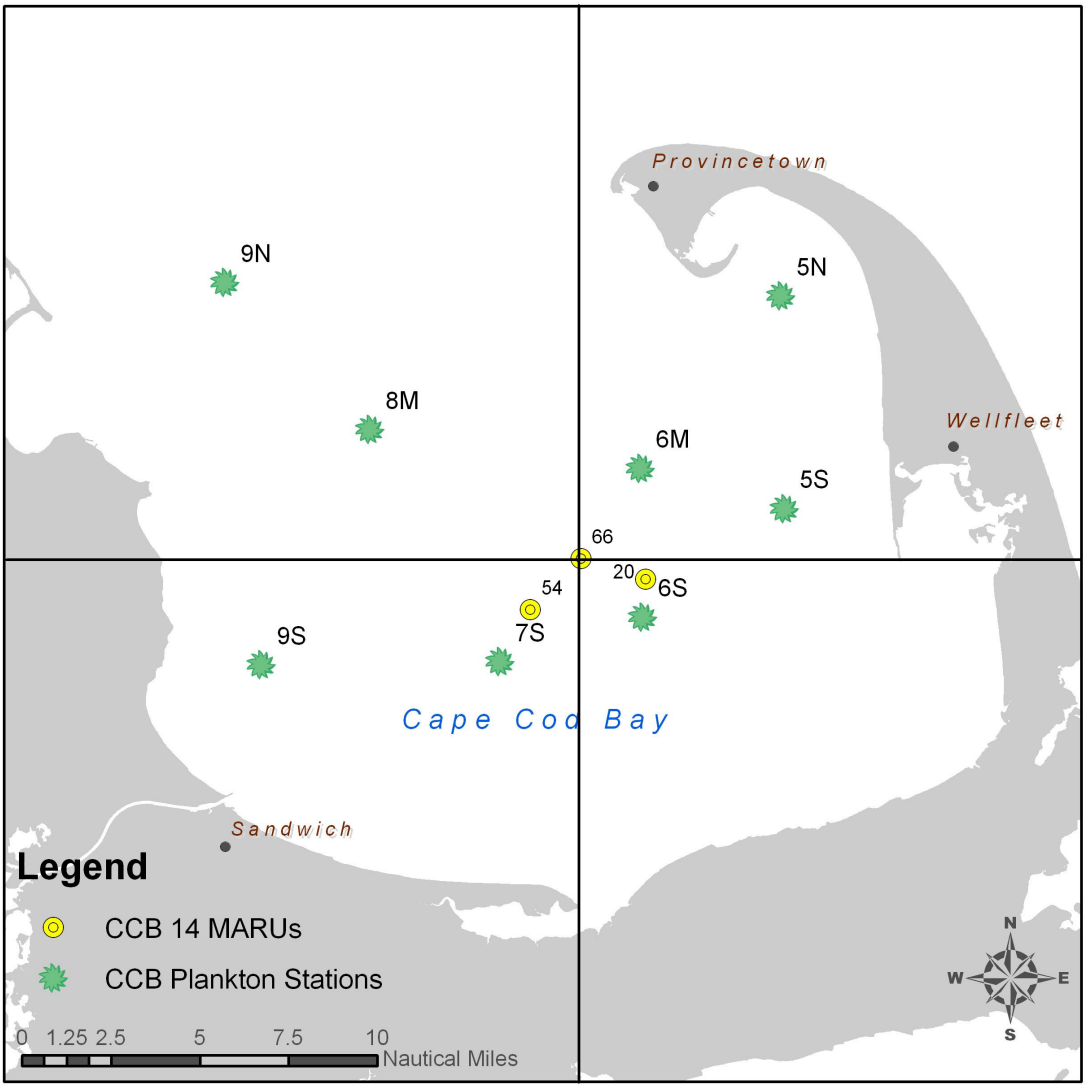

Figure 4 Cape Cod Bay MARU and plankton sampling stations for the CCB 14 deployment, during which acoustic data were recorded in 2005.

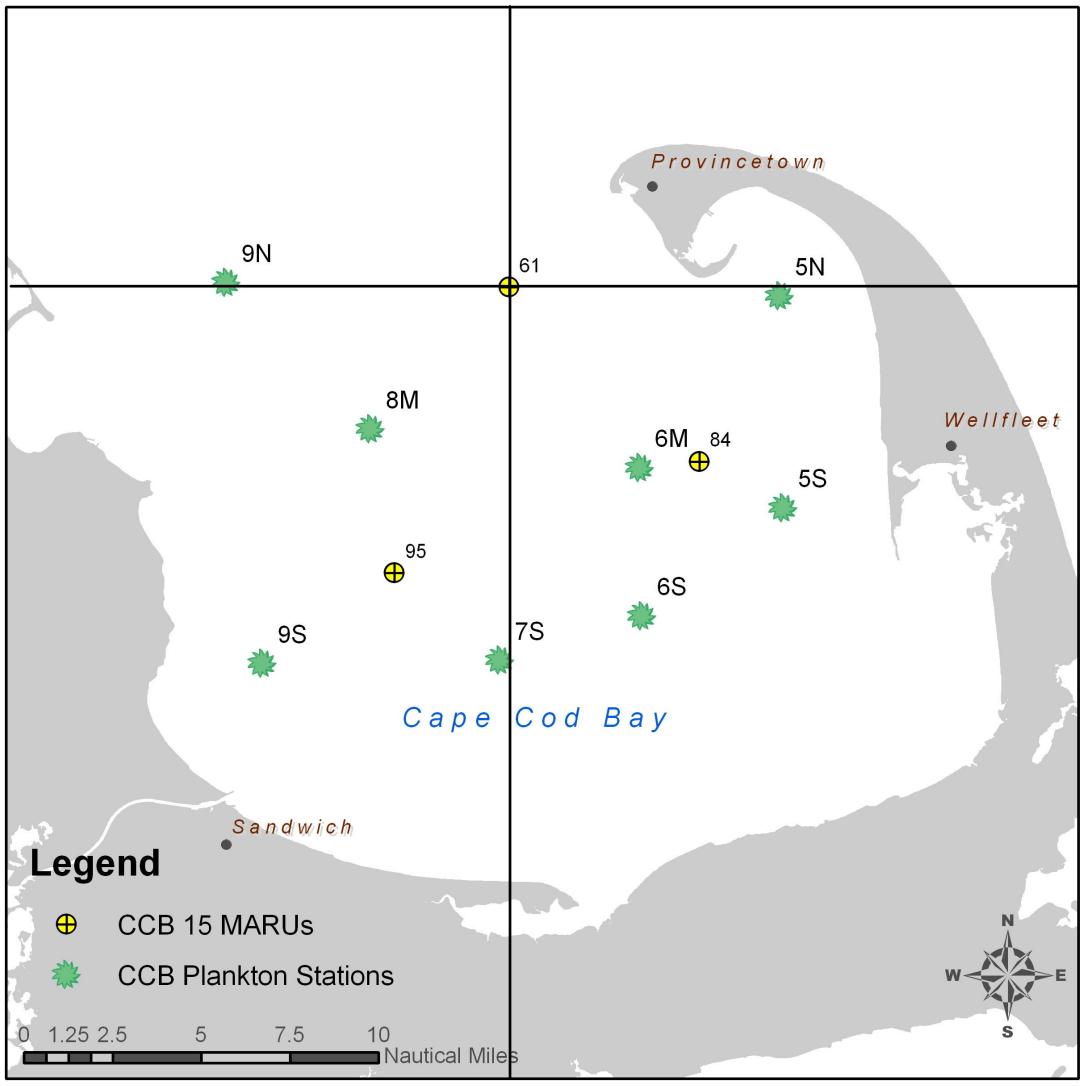

Figure 5 Cape Cod Bay MARU and plankton sampling stations for the CCB 15 deployment, during which acoustic data were recorded in 2006.

To analyze the acoustic recordings, I used XBAT (Figueroa 2008) and ISRAT_LT (Urazghildiiev and Clark 2007), both MATLAB software programs. First, I used XBAT to display the sound files in spectrographic view. Then, I either verified all calls marked in the XBAT log files that existed for the sample day, or, if a log file did not exist for the sound, I browsed the sound file and created a log file containing all right whale calls for the day (Figure 6).

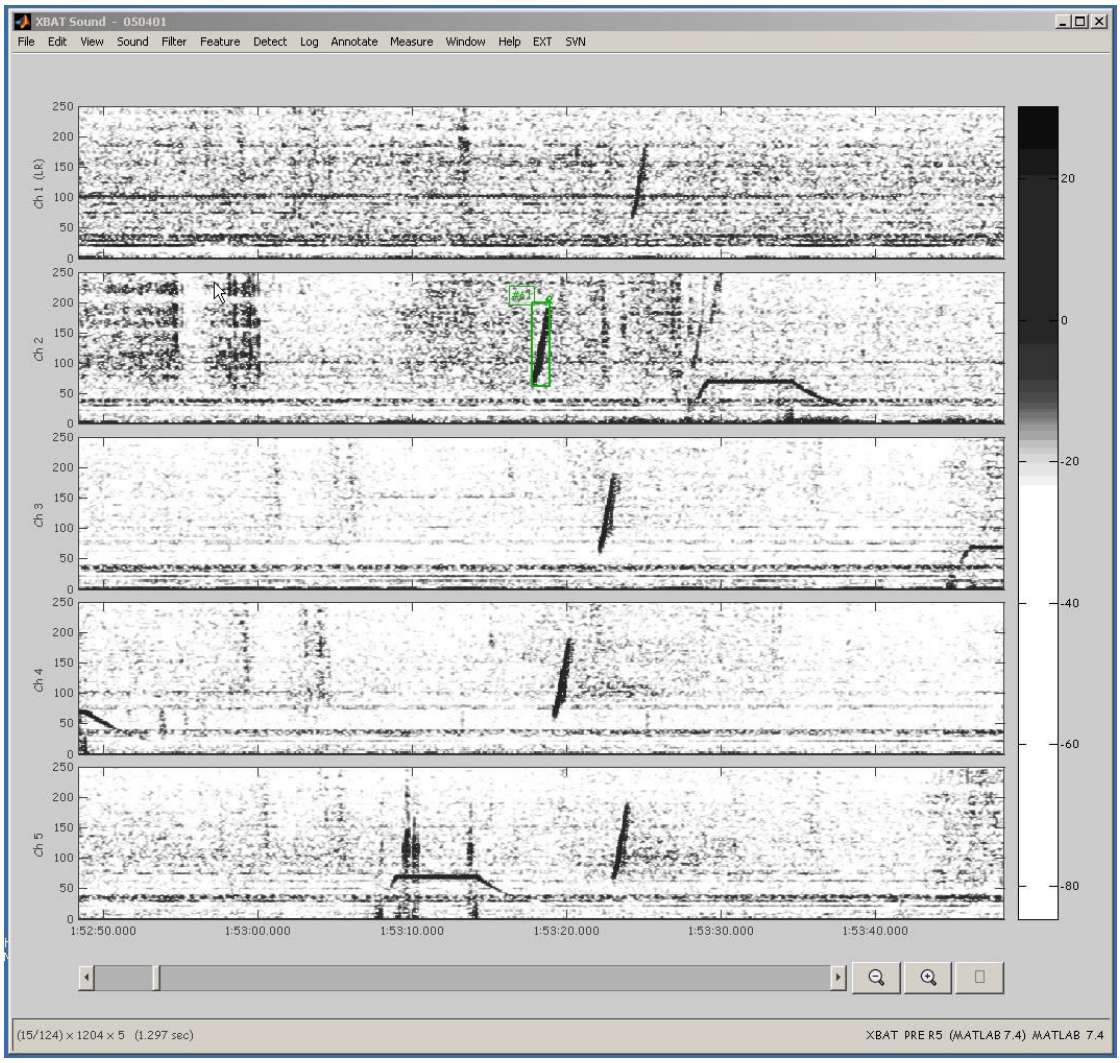

Figure 6 XBAT is the MATLAB program used to browse the acoustic recordings and mark North Atlantic right whale call events (Figueroa 2008).

The number of right whale calls included in the XBAT log file was the number that I used for the bay aggregate models. After tabulating all right whale calls from the sound files for all eleven days in the study, I used ISRAT_LT (Figure 7), a location software program, to assign a bearing to each logged call that was recorded on at least 3 MARUs.

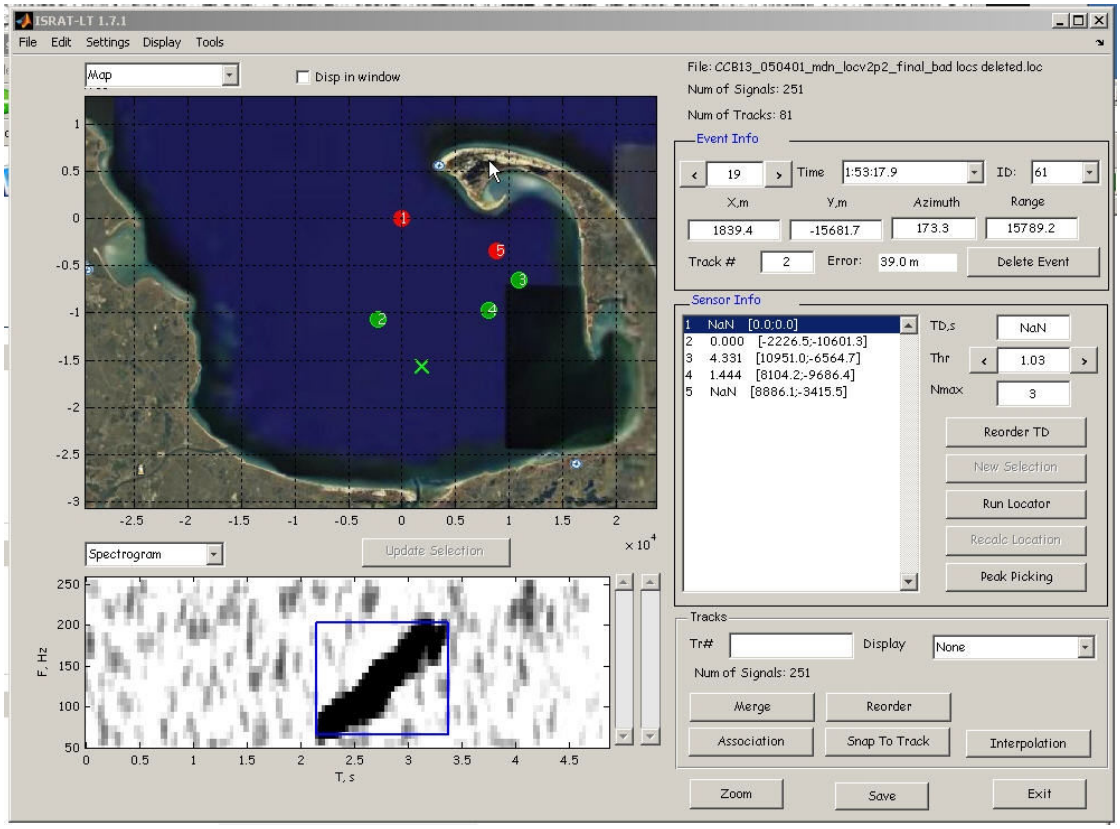

Figure 7 ISRAT_LT is the MATLAB program used to calculate and assign bearings for each call event (Urazghildiiev and Clark 2007; Urazghildiiev and Clark 2007).

Statistics

To determine if region, day, year, zooplankton density, or the interaction between zooplankton density and year had an effect on the number of right whale calls per region, I transformed the number of right whale calls to the log scale. I used JMP to model the data using a general linear model (GLM), using food as a continuous

variable (JMP 2008). I used log (calls + 1) as the y variable for all GLMs that I ran. I accounted for the effects of year, day, region, zooplankton density, and the interaction between zooplankton density and year. Zooplankton density was represented using several different zooplankton parameters: early surface *Calanus* (stages I-IV); late surface *Calanus* (stages V-VI); total surface *Calanus*; and surface zooplankton (all species) total. The units for zooplankton density were the total number of individual zooplankton per cubic meter. I treated region and day as random effects and year and zooplankton as fixed effects (Models 1-5).

To determine if day, year, zooplankton density, or the interaction between zooplankton density and year had an effect on the number of right whale calls for the entire bay, I transformed the number of right whale calls to the log scale. I used JMP to model the data using a GLM with food as a continuous variable. I used log (calls + 1) as the y variable. I accounted for the effects of year, day, zooplankton density, and the interaction between zooplankton density and year. The units for zooplankton density were the total number of individual zooplankton per cubic meter. I treated day as a random effect and year and zooplankton as fixed effects (Model 6).

I used GLMs to model the effect of year on zooplankton density (Model 7) and the effect of day on zooplankton density (Model 8).

Results

Models 1-4

1. When accounting for the effects of region, day, year, early surface *Calanus* density, and the interaction between early surface *Calanus* density and year, I found that the when the effects of 2003, 2005, and 2006 were combined, early surface *Calanus* density and the interaction between early surface *Calanus* density and year have no effect on the number of calls (p-values 0.16, 0.26, 0.48).

2. When accounting for the effects of region, day, year, late surface *Calanus* density, and the interaction between late surface *Calanus* density and year, I found that the effect of the three years combined, late surface *Calanus* density and the interaction between late surface *Calanus* density and year have no effect on the number of calls (p-values 0.12, 0.73, 0.36). However, when looking only at years 2003 and 2006, year has an effect on number of calls (p-value 0.05).

3. When accounting for the effects of region, day, year, surface *Calanus* total, and the interaction between surface *Calanus* total and year, I found that the effect of the three years combined, surface *Calanus* total, and the interaction between surface *Calanus* total and year have no effect on the number of calls (p-values 0.14, 0.24, 0.43).

4. When accounting for the effects of region, day, year, surface zooplankton total density, and the interaction between surface zooplankton total density and year, I found that the effect of the three years combined, surface zooplankton total density, and the interaction between surface zooplankton total density and year have no effect on the number of calls (p-values 0.10, 0.29, 0.63). However, when looking only at years 2003 and 2006, year has an effect on number of calls (p-value 0.04).

The above GLMs showed that day has a minimal effect on zooplankton density, which suggests that by taking the average yearly regional zooplankton density and the average yearly regional call count and using single data points for each year to model call counts using zooplankton density, region, year, and the interaction between zooplankton density and year, daily effects are not lost (Model 5) because day to day differences in early surface *Calanus*, late surface *Calanus*, total surface *Calanus*, and total surface zooplankton contributed to only 29.23%, 28.06%, 29.39%, and 28.14%of the variability in the data, respectively.

Model 5

5. For the fifth GLM, I calculated the average number of right whale up calls per region per day for each year and then transformed the average to the log scale. I also calculated the average total zooplankton density per day per region for each year. I used log (calls + 1) as the y variable, which was continuous, for the GLM. The data point for zooplankton density was calculated by averaging the daily CCB aggregate measurements over each year. I treated region as a random effect. Year and CCB total zooplankton surface density were treated as fixed effects. After controlling for effects of region, year, surface zooplankton total density, and the interaction between surface zooplankton total density and year, I found that year does have an effect on number of calls (p-value 0.05).

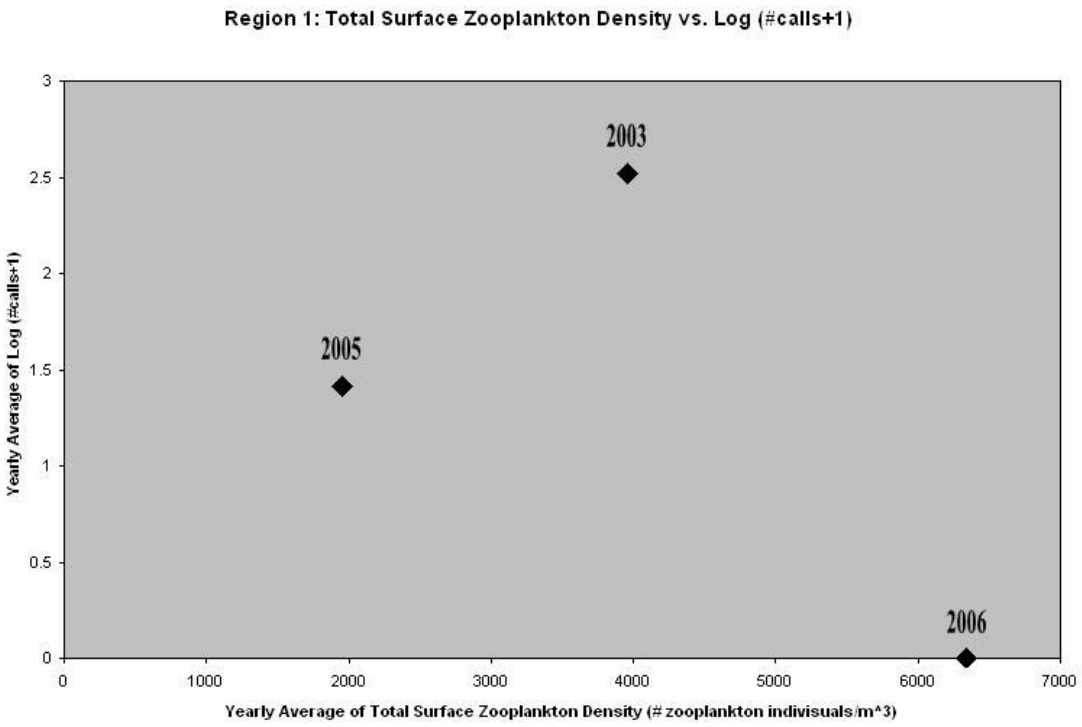

Figure 8 For Model 5, year does have an effect on number of calls (p-value 0.05). This figure displays the yearly average of total surface zooplankton density (# zooplankton individuals/m^3) plotted against yearly average of log (#calls+1) for Region 1.

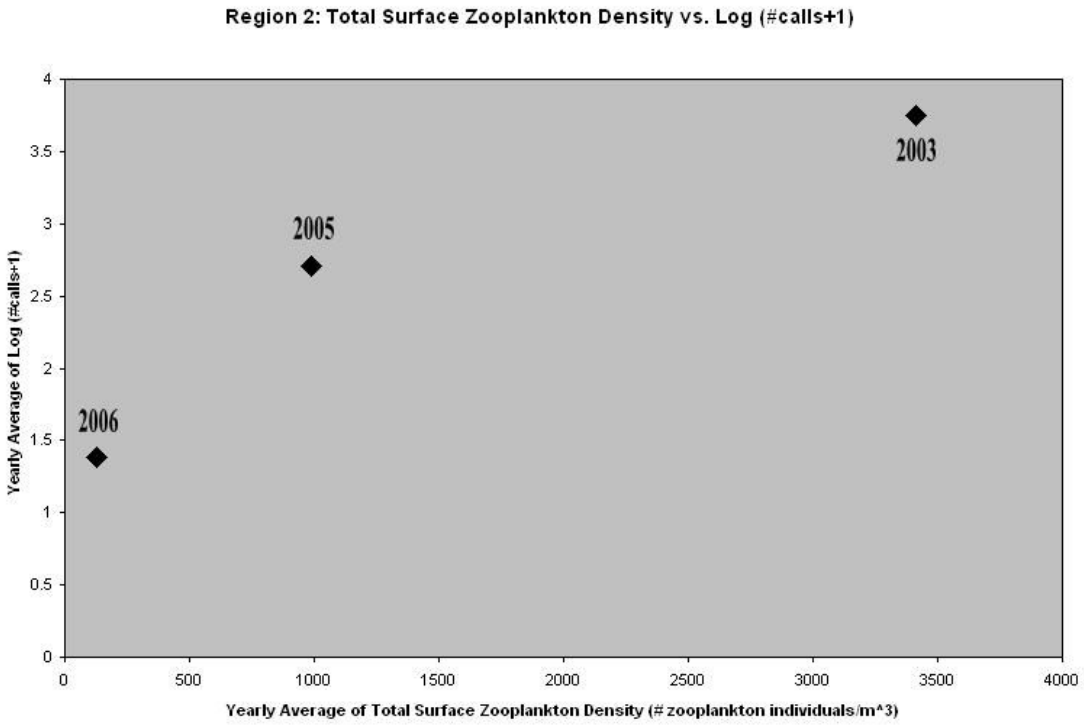

Figure 9 For Model 5, year does have an effect on number of calls (p-value 0.05). This figure displays the yearly average of total surface zooplankton density (# zooplankton individuals/m^3) plotted against yearly average of log (#calls+1) for Region 2.

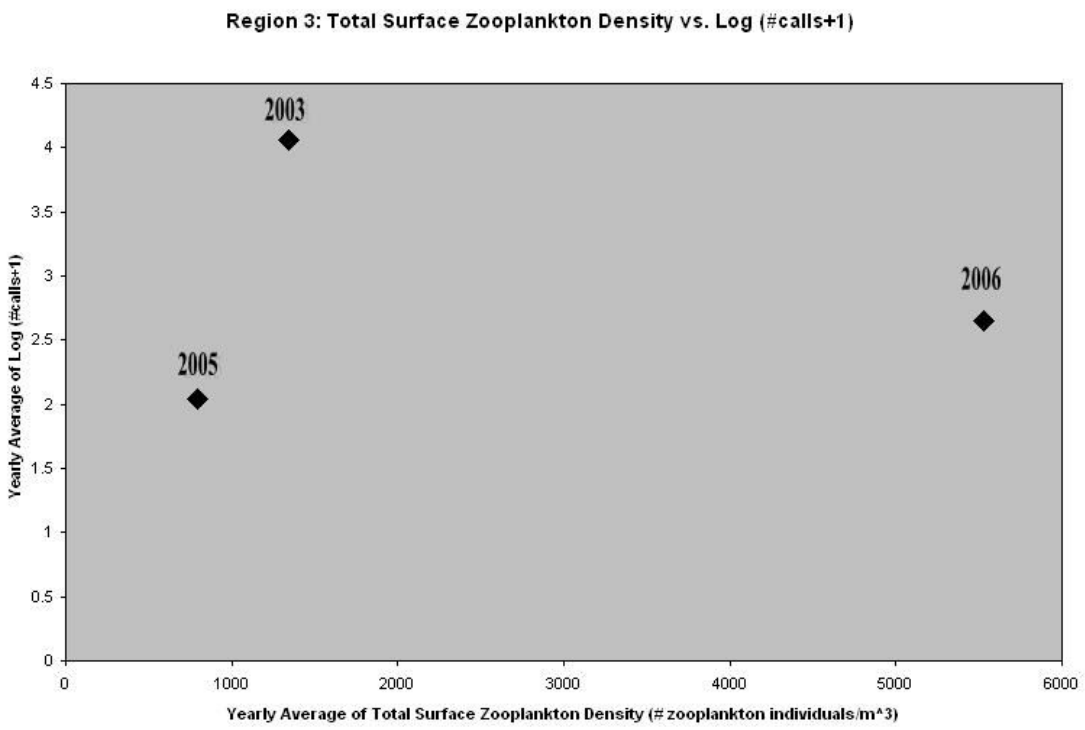

Figure 10 For Model 5, year does have an effect on number of calls (p-value 0.05). This figure displays the yearly average of total surface zooplankton density (# zooplankton individuals/m^3) plotted against yearly average of log (#calls+1) for Region 3.

Model 6

6. When accounting for the effects of day, year, zooplankton density for the entire bay, and the interaction between zooplankton density for the entire bay and year, I found that year, zooplankton density for the entire bay, and the interaction between zooplankton density for the entire bay and year do not have an effect on the number of calls in the entire bay (p-values 0.86, 0.75, 0.91).

Model 7

7. There was no significant interaction between early surface *Calanus*, late surface *Calanus*, surface *Calanus* total, or surface zooplankton (all species) total and year (p-values 0.48, 0.36, 0.43, 0.63).

Model 8

8. The effect of day on early surface *Calanus*, late surface *Calanus*, total surface *Calanus*, and surface zooplankton (all species) total was responsible for only a small percentage of variability in the data (19.07%, 3.35%, 18.24%, and 23.41%, respectively).

Discussion

Models 1-4:

Though overall, the JMP models suggest that zooplankton density does not affect call number at the regional or bay level, when using surface late *Calanus* (stages V-VI) density and surface zooplankton total density as model effects, surface late *Calanus* density and surface zooplankton total density have an effect on right whale call number when only the years 2003 and 2006 are included in the model. This effect may be stronger with the surface late *Calanus* density because these samples contain the zooplankton individuals that are at the life stage that right whales prefer to eat. This effect may be greater for surface zooplankton total because in addition to *Calanus*, other species eaten by right whales, such as *Pseudocalanus* and *Centropages typics* (Baumgartner 2007) are included in the model.

The results from *Models 2* and *4* suggest that year does have an effect on call number, and therefore, call number may be indirectly related to zooplankton density; however, this relationship is unclear. In *Models 1-4*, day and region do not significantly affect call number. These results support the decision to calculate yearly averages for zooplankton densities and right whale call numbers from each region and to model call number using yearly averages. Additionally, the results support modeling call number for the entire bay using zooplankton densities for the entire bay.

The above GLMs showed that day has a minimal effect on zooplankton density, which justifies taking the average yearly total surface zooplankton density and the average yearly regional call count and using single data points for each year to model call counts using zooplankton density, region, year, and the interaction between zooplankton density and year (Model 5). Day to day differences contributed to only 29.23%, 28.06%, 29.39%, and 28.14% of the variability in the data.

The results from these models support the alternative hypothesis that North Atlantic right whales do not acoustically advertise food resources.

Model 5:

By averaging data from each region over an entire year, it is possible that subtle increases and decreases in zooplankton densities and call numbers, which might have demonstrated correlation at small, location-specific scales, were lost, resulting in a lower probability that a significant relationship between zooplankton density and call number would appear. However, Model 5 did demonstrate that year does have an effect on call number when only the years 2003 and 2006 are compared. As mentioned before, the year effect may be indirectly related to zooplankton density.

Model 6:

As when the yearly averages for regions were modeled, when averaging the zooplankton densities and call numbers for the entire bay for each year and modeling the effects of day, year, zooplankton density for the entire bay, and the interaction between zooplankton density for the entire bay and year on call number for the entire bay, the subtleties for region-specific zooplankton densities and potentially associated call numbers may have been lost, resulting in a lower probability that there would be a correlation between zooplankton density and call number.

Neither year nor day had a significant effect on zooplankton density. Perhaps part of the reason that zooplankton density does not have a significant effect on call number is that only a narrow range of zooplankton densities were represented across days and years, making it difficult to test the effect of zooplankton on call rate.

To account for the potential errors caused by analysis at a regional level, I conducted studies with the plankton and acoustic readings from the entire bay combined. This approach allowed zooplankton density and calls from the entire bay to be compared, without the potential errors created by regional divisions. However, at the bay aggregate level, zooplankton density and calling behavior were not correlated.

North Atlantic right whales have been recorded during all seasons and throughout their migratory range, in both feeding and non-feeding habitats. Therefore, in CCB during the winter months, acoustic communication may serve a broad range of purposes, including feeding, or serve a non-feeding purpose. Additional explanations for right whale acoustic activity in CCB include locating mates, maintaining acoustic contact with young, socializing, navigation, or a currently undetermined function.

North Atlantic right whales may not be using intraspecific acoustic communication to locate food resources. Perhaps they are using environmental cues such as temperature, salinity, chemosensory cues, or acoustic cues from fish and/or birds (Kenney 2001).

Several weaknesses in my research methodology could have clouded the project's results. First, only a total of eleven days from three different years were analyzed. Ideally, many more days from each existing year and days from additional years would have been analyzed for the study. Secondly, the MATLAB software program used to assign calls to regions has not been extensively calibrated and there is

some error associated with results**.** Additionally, during the analysis process of assigning calls to a region, the quality of some recordings prohibited the assignment of a call to a region, and these calls were deleted and therefore not incorporated in the final statistical analyses. I assumed that these omissions were spread evenly across the samples. However, it is possible that they were not, causing the number of calls on certain days to be under or over represented in comparison to the other days.

I arbitrarily divided CCB into three quadrants into which to assign calls and zooplankton densities (Figures 1 - 5). The value for zooplankton for a specific region was generated by selecting the zooplankton sampling station most centrally located within the region and using the zooplankton density reading collected from that station. However, even if a station were located directly in the center of the region, the calls located on the edge of the region could have been equally close or closer to other zooplankton sampling stations. Therefore, the zooplankton densities that were compared to the number of calls recorded in the region over the sampling time period may not have been the most representative zooplankton density for that region. For example, though when possible the sampling station associated with a region was in the center of the region, sometimes the only station from which readings were available was near the border of a region. This means that the zooplankton sampling station could have been closer to calling whales outside the region than some of the acoustic sources within the region.

To model the relationship between zooplankton and right whale acoustic behavior, I first used a regional scale analysis unit, assuming that if the regional relationship between zooplankton densities and right whale call numbers was used, the number of right whale calls would be more reflective of the local zooplankton resources. However, when assigning calls to a region, I kept only calls that were recorded on 3 or more MARUs because they provided the most reliable bearings. I

assumed that these deletions were spread evenly over the data set; however, they may not have been, resulting in a source of error.

If the PCCS did not collect a zooplankton sample for all regions in the bay on the same day, but did collect samples from all regions in the bay during a similar time frame, I used the zooplankton sample taken on the date closest to the day that the other zooplankton samples and associated acoustic samples were collected. The geographical and time incoherence between zooplankton and acoustic samples could have obscured the relationship between zooplankton and right whale calls.

Another variable that may have skewed the study is that the PCCS research vessel was active in CCB every day during which a plankton sample was collected, which means that each day included in the sample was a day during which boat noise was present in CCB. If boat noise affects right whale acoustic behavior, the boat noise could have resulted in modified right whale acoustic behavior for each day sampled in the study. Additionally, boat presence and the zooplankton sample collection procedure could have changed the actual density of zooplankton present in the water column.

North Atlantic right whales are known to make three types of sounds: up calls, social sounds, and gun shots. However, for this study, I only tabulated and accounted for up calls, and not social calls or gunshot calls. Therefore, if right whales are making calls other than up calls while feeding, those calls would not have been accounted for when modeling the effect of zooplankton on acoustic behavior.

North Atlantic right whales swim at approximately 1.5 m/s while feeding (Hammer 1988; Werth 2004). Therefore, right whales could swim from one side of CCB to the other in one day. If right whales are moving through more than one region during one day, then modeling zooplankton density and call rate on the regional scale

is not representative of the daily relationship between food availability to and acoustic behavior of right whales in the bay.

Copepods, the right whales' food source, may only congregate in the densities required for right whale feeding for a limited time. Time of zooplankton sampling was not included in the data set that I was provided with. Therefore, it was not possible to isolate the specific time window when the zooplankton sample was collected. Instead, I used the total number of calls recorded during the entire day that the zooplankton sample was collected to calculate the call number that I used in the JMP models. Consequently, if the zooplankton resource dissipated shortly after the sample was collected, the model results would not reflect that change in zooplankton density when calculating the effect of zooplankton density on right whale calling behavior. To account for the lack of time coordination between acoustic and zooplankton sampling, researchers should count only right whale calls that were recorded within the operating hours of the PCCS vessel, which would be approximately 08:00 to 16:00 hours

Zooplankton density is used in this research as an indicator of feeding behavior. However, zooplankton density may not be a reliable indicator of feeding behavior. Zooplankton density must be at least 4000 individuals per cubic meter for it to be energetically worthwhile for right whales to open their mouths to feed (Mayo 1992). However, only 5 out of 33 data points contained zooplankton densities equal to or higher than 4000 individuals per cubic meter. To accurately test for the effect of zooplankton density on right whale acoustic behavior, additional acoustic analyses should be conducted to increase the number of sample units with zooplankton densities equal to or higher than 4000 individuals per cubic meter.

For this study, I have assumed that right whales prefer feeding on zooplankton at the surface rather than on those in the water column. Therefore, I have only

modeled the relationship between surface zooplankton density and right whale calls. However, the PCCS also collected oblique (full water column) zooplankton samples, which should be considered in future analyses.

In this study, the results supported the alternative hypothesis: North Atlantic right whales do not acoustically advertise food resources. However, additional research would clarify whether this hypothesis holds, or whether a greater sample size would yield different results. I recommend the following suggestions for future research to study the correlation between zooplankton density and North Atlantic right whale acoustic behavior:

1. Increase the number of sample days, including adding more days for each year and more years.
2. Collect acoustic data in the same locations each year.
3. Delineate regions so that the zooplankton sampling station for each region is located within the center of the region.
4. Include only days with zooplankton readings of 4000 or more individuals per cubic meter.
5. Record the time that zooplankton samples are collected so that zooplankton densities can be compared to call numbers recorded within a four hour window around the time that zooplankton samples were collected.
6. Include all calls types (up, social, gunshot) in the total call count.
7. Calculate the effect of zooplankton density on call type proportion.
8. Track whales and model effect of zooplankton density on the number of calls per individual.

Additional ideas that would be interesting to pursue in future studies of the relationship between zooplankton availability and North Atlantic right whale acoustic behavior:

1. Is there a delay in time between changes in zooplankton density and/or right whale feeding activity and right whale acoustic behavior?
2. Do factors such as diurnal effect, tide, season, behavioral context, ambient noise level, or oceanographic condition affect zooplankton density and right whale acoustic behavior?

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